DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

Fishery Bulletin

Vol. 80, No. 4 October 1982

In Memoriam—Thomas A. Manar 653
MILLIKIN, MARK R. Qualitative and quantitative nutrient requirements of fishes: A review 655
WETHERALL, JERRY A. Analysis of double-tagging experiments 687
BURGESS, LOURDES ALVINA. Four new species of squid (Oegopsida: *Enoploteuthis*) from the central Pacific and a description of adult *Enoploteuthis reticulata* 703
CREASER, EDWIN P., and DAVID A. CLIFFORD. Life history studies of the sandworm, *Nereis virens* Sars, in the Sheepscot Estuary, Maine 735
LANGTON, RICHARD W. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish.. 745
HETTLER, WILLIAM F., and ALEXANDER J. CHESTER. The relationship of winter temperature and spring landings of pink shrimp, *Penaeus duorarum*, in North Carolina 761
ALLEN, LARRY G. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California 769
BOTSFORD, LOUIS W., RICHARD D. METHOT, JR., and JAMES E. WILEN. Cycle covariation in the California king salmon, *Oncorhynchus tshawytscha*, silver salmon, *O. kisutch*, and Dungeness crab, *Cancer magister*, fisheries 791
WEBB, P. W., and RAYMOND S. KEYES. Swimming kinematics of sharks.. 803
BEACHAM, TERRY D., and PAUL STARR. Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia 813
LAROCHE, JOANNE LYCZKOWSKI. Trophic patterns among larvae of five species of sculpins (Family: Cottidae) in a Maine estuary 827
PETERSON, WILLIAM T., RICHARD D. BRODEUR, and WILLIAM G. PEARCY. Food habits of juvenile salmon in the Oregon coastal zone, June 1979 841
COLIN, PATRICK L. Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae) 853
WALTZ, C. WAYNE, WILLIAM A. ROUMILLAT, and CHARLES A. WENNER. Biology of the whitebone porgy, *Calamus leucosteus*, in the South Atlantic Bight 863
WATKINS, WILLIAM A., and WILLIAM E. SCHEVILL. Observations of right whales, *Eubalaena glacialis*, in Cape Cod waters 875

(Continued on back cover)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE
Malcolm Baldrige, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
John V. Byrne, *Administrator*

NATIONAL MARINE FISHERIES SERVICE
William G. Gordon, *Assistant Administrator*

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

EDITOR

Dr. Carl J. Sindermann
Scientific Editor, *Fishery Bulletin*
Northeast Fisheries Center Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

Editorial Committee

Dr. Bruce B. Collette
National Marine Fisheries Service

Dr. Edward D. Houde
Chesapeake Biological Laboratory

Dr. Merton C. Ingham
National Marine Fisheries Service

Dr. Reuben Lasker
National Marine Fisheries Service

Dr. Donald C. Malins
National Marine Fisheries Service

Dr. Jerome J. Pella
National Marine Fisheries Service

Dr. Jay C. Quast
National Marine Fisheries Service

Dr. Sally L. Richardson
Gulf Coast Research Laboratory

Mary S. Fukuyama, Managing Editor

The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Bin C15700, Seattle, WA 98115. Second class postage paid to Finance Department, USPS, Washington, DC 20260.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department.

Fishery Bulletin

CONTENTS

Vol. 80, No. 4 October 1982

In Memoriam—Thomas A. Manar 653
MILLIKIN, MARK R. Qualitative and quantitative nutrient requirements of fishes: A review 655
WETHERALL, JERRY A. Analysis of double-tagging experiments 687
BURGESS, LOURDES ALVINA. Four new species of squid (Oegopsida: *Enoploteuthis*) from the central Pacific and a description of adult *Enoploteuthis reticulata* 703
CREASER, EDWIN P., and DAVID A. CLIFFORD. Life history studies of the sandworm, *Nereis virens* Sars, in the Sheepscot Estuary, Maine 735
LANGTON, RICHARD W. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish .. 745
HETTLER, WILLIAM F., and ALEXANDER J. CHESTER. The relationship of winter temperature and spring landings of pink shrimp, *Penaeus duorarum*, in North Carolina 761
ALLEN, LARRY G. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California 769
BOTSFORD, LOUIS W., RICHARD D. METHOT, JR., and JAMES E. WILEN. Cycle covariation in the California king salmon, *Oncorhynchus tshawytscha*, silver salmon, *O. kisutch*, and Dungeness crab, *Cancer magister*, fisheries 791
WEBB, P. W., and RAYMOND S. KEYES. Swimming kinematics of sharks .. 803
BEACHAM, TERRY D., and PAUL STARR. Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia 813
LAROCHE, JOANNE LYCZKOWSKI. Trophic patterns among larvae of five species of sculpins (Family: Cottidae) in a Maine estuary 827
PETERSON, WILLIAM T., RICHARD D. BRODEUR, and WILLIAM G. PEARCY. Food habits of juvenile salmon in the Oregon coastal zone, June 1979 841
COLIN, PATRICK L. Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae) 853
WALTZ, C. WAYNE, WILLIAM A. ROUMILLAT, and CHARLES A. WENNER. Biology of the whitebone porgy, *Calamus leucosteus*, in the South Atlantic Bight 863
WATKINS, WILLIAM A., and WILLIAM E. SCHEVILL. Observations of right whales, *Eubalaena glacialis*, in Cape Cod waters 875

(Continued on next page)

Seattle, Washington

1982

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402—Subscription price per year: $15.00 domestic and $18.50 foreign. Cost per single issue: $4.50 domestic and $5.65 foreign.

Notes

BOEHLERT, GEORGE W., W. H. BARSS, and P. B. LAMBERSON. Fecundity of the widow rockfish, *Sebastes entomelas*, off the coast of Oregon 881

BABINCHAK, JOHN A., DANIEL GOLDMINTZ, and GARY P. RICHARDS. A comparative study of autochthonous bacterial flora on the gills of the blue crab, *Callinectes sapidus*, and its environment 884

LE BOEUF, BURNEY J., MARIANNE RIEDMAN, and RAYMOND S. KEYS. White shark predation on pinnipeds in California coastal waters 891

SCHLOTTERBECK, ROBERT E., and DAVID W. CONNALLY. Vertical stratification of three nearshore southern California larval fishes (*Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*)............ 895

LIBBY, DAVID A. Decrease in length at predominant ages during a spawning migration of the alewife, *Alosa pseudoharengus*............ 902

GOLDBERG, STEPHEN R. Seasonal spawning cycle of the longfin sanddab, *Citharichthys xanthostigma* (Bothidae) 906

ROBINSON, GARY R. Otter trawl sampling bias of the gill parasite, *Lironeca vulgaris* (Isopoda, Cymothoidae), from sanddab hosts, *Citharichthys* spp....... 907

INDEX, VOLUME 80 911

Notices

NOAA Technical Reports NMFS published during the first 6 months of 1982

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

IN MEMORIAM

Thomas A. Manar

1912-1982

Thomas Alonzo (Lon) Manar, former Chief of the Scientific Publications Staff (now the Scientific Publications Office), died at his home in Encinitas, Calif., on 26 August 1982 after a heart seizure. Lon Manar was a journalist, newspaperman, science writer, and editor in the best traditions of his craft. As the Chief of the Scientific Publications Staff in Seattle, Wash., from 1970 to 1974, he set the style and format for a revamped U.S. Fishery Bulletin. The early years of the Marine Fisheries Review also reflected his flair for innovative and creative journalism. In 1974 his superior service and unique talents were recognized with the award of a Bronze Medal by the U.S. Department of Commerce.

A graduate in journalism from the University of Oklahoma, Mr. Manar joined the Scripps Institution of Oceanography as scientific editor in 1951 after a stint as a meteorologist in the U.S. Army during World War II and as a newspaperman in Oklahoma. In the early 1960's he set up the public information office at the University of California, San Diego when the campus was developing.

In 1965, following the death of his wife, Ruth, Mr. Manar left the University for a position with the Federal Government as Chief of Publication Services for the Bureau of Commercial Fisheries Biological Laboratory in Honolulu, Hawaii; until 1970 he lived and worked in Honolulu. His last position before retirement was as an editor and consultant with the Southwest Fisheries Center of the National Marine Fisheries Service, NOAA, in La Jolla, Calif.

Mr. Manar was a man of wide interests and enthusiasm—art, music, reading, nature photography. After his retirement he traveled extensively in this country and abroad. He is survived by a sister, Maurine Manar of Encinitas.

While Mr. Manar was not a fishery biologist, he understood scientists and their needs. Many manuscripts arrived on his desk in shambles and emerged as examples of good scientific writing. Those of us who benefited from his talents are grateful; the Fishery Bulletin has benefited the most.

QUALITATIVE AND QUANTITATIVE NUTRIENT REQUIREMENTS OF FISHES: A REVIEW[1]

MARK R. MILLIKIN[2]

ABSTRACT

Qualitative and quantitative protein, amino acid, lipid, fatty acid, carbohydrate, vitamin, and mineral requirements are summarized for salmonids and warmwater fish species. Special emphasis is placed upon amino acid, vitamin, and mineral requirements of fishes, since recent research with these nutrients has contributed to a better understanding of fish physiology and nutritional requirements. Protein requirements of fishes briefly stated are as follows: 30 to 55% dietary protein dependent upon age and feeding habit and dietary essential amino acids which include arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine. Dietary lipid concentrations as high as 12 to 24% have demonstrated sparing action of protein for growth rather than energy utilization in fishes. Essential fatty acids for fishes usually include linolenic acid or an elongated form in the $\omega 3$ fatty acid family, while some fish species appear to derive nutritional benefit from linoleic acid. Vitamins required by fishes in the diet include thiamine, riboflavin, pyridoxine, niacin, pantothenic acid, ascorbic acid, choline, folic acid, cyanocobalamin, biotin, inositol, vitamin A, cholecalciferol, vitamin E, and vitamin K. Minerals required in the diet of fishes include phosphorus, magnesium, and trace amounts of manganese, zinc, iron, copper, selenium, and iodine. Carbohydrate is an important dietary energy source for herbivorous and omnivorous species and can be incorporated into diets of carnivorous species for protein sparing action at slightly higher concentrations than those occurring in their natural diets.

A paucity of information exists concerning qualitative and quantitative nutrient requirements of various life stages of several species currently reared in large quantities in fish hatcheries. Interactions of various macronutrients and micronutrients as related to artificial diet formulation for fish culture are also discussed. Additionally, recommendations for future research are outlined.

Determination of nutrient requirements for fishes fed formulated diets has contributed to healthier, more rapidly growing fishes cultured in hatcheries and commercial facilities. For instance, formulated diets designed specifically for several salmonid species and channel catfish, *Ictalurus punctatus*, have been instrumental in the recent growth of salmon, trout, and catfish commercial culture. Recent production values of catfish, trout, and salmon by aquaculture in the United States are listed in Table 1. Information has also been gained on many physiological similarities and differences between fishes and other aquatic and terrestrial species.

TABLE 1.—United States aquaculture production of catfish, trout, and salmon, 1979 and 1980.[1]

	1979		1980	
Species	Metric tons	Thousands dollars	Metric tons	Thousands dollars
Catfish	18,415.9	28,800	34,790.6	53,600
Salmon	1,088.6	900	3,447.3	3,400
Trout	11,339.8	21,000	21,772.5	37,500

[1] Adapted from Thompson (1981). Data represent live weight harvest for consumption. Excluded are eggs, fingerlings, and other intermediate products.

Reviews dealing with nutrient requirements of fishes include those by Halver (1972a) and the National Research Council (1973, 1977, 1981). Halver (1972a) dealt with macro- and micronutrient requirements of fishes, known and proposed biochemical pathways in fishes, feed formulation strategy, fish cultural practices, and feeding aspects of fish culture. However, since this thorough description of nutrient requirements of fishes, much additional information has been gained on fish nutrition. Synopses have been compiled of chemical composition of feed ingredients commonly used in formulated fish feeds, recommended test diet ingredient composition for determination of nutrient requirements of fishes, and feed formulation strategies on use of various combinations of protein or lipid sources (National Research Council 1973, 1977, 1981). Brief reviews of qualitative and quantita-

---

[1] Contribution No. 82-13C, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Charleston, S.C.

[2] Southeast Fisheries Center Charleston Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 12607, Charleston, SC 29412.

Manuscript accepted April 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

tive nutrient requirements for specific groups of fishes are available. Included are those for trout, salmon, and catfish (National Research Council 1973), warmwater fishes such as common carp, *Cyprinus carpio*, channel catfish (National Research Council 1977), and salmonids (National Research Council 1981). Cowey and Sargent (1979) reviewed recent advances in protein, lipid, amino acid, fatty acid, vitamin, and mineral requirements of fishes, since their earlier work (Cowey and Sargent 1972). Special emphasis was placed on biochemical pathways in fish. However, only selected vitamin and mineral nutrient requirements of fishes were discussed, and no attempt was made to summarize, in total, the nutrient requirements of fishes. Also, a brief review of qualitative amino acid, fatty acid, vitamin, and mineral requirements of fishes is available in tabular form (Ketola 1977).

Currently, there is a paucity of information on nutrient requirements of fry and fingerling stages of coolwater fishes having commercial or recreational value (Ketola 1978; Orme 1978). Such species include the largemouth bass, *Micropterus salmoides*; smallmouth bass, *M. dolomieui*; yellow perch, *Perca flavescens*; northern pike, *Esox lucius*; muskellunge, *E. masquinongy*; tiger muskie hybrid (male northern pike × female muskellunge); and walleye, *Stizostedion vitreum vitreum*. Also, nutrient requirements for striped bass, *Morone saxatilis*, (a coolwater or warmwater species depending upon the region of occurrence) are lacking except for protein requirements of the fingerling stage as a function of dietary lipid content (Millikin in press).

The present review provides an updated summary of qualitative and quantitative protein, amino acid, lipid, fatty acid, vitamin, and mineral requirements for all groups of fishes. Nutritive values of various feedstuffs, e.g., protein and lipid sources, and their relative contributions to cost-effective feed formulation, are not covered in this review.

Some topics important in fish nutrition that are not reviewed in the present article are metabolizable energy values of specific nutrients and feedstuffs for fishes and antinutritional factors often occurring in certain feedstuffs incorporated into commercial fish feeds. Metabolizable energy values of rainbow trout, *Salmo gairdneri*, have been examined for carbohydrates (Smith 1971), proteins (National Research Council 1981), and feedstuffs (Smith 1976; Smith et al. 1980; National Research Council 1981). Also, variability in heat increment as a portion of metabolizable energy resulting from protein, carbohydrate, or lipid ingestion was examined in rainbow trout and Atlantic salmon, *S. salar*, fingerlings (R. R. Smith et al. 1978). Important antinutritional factors often occurring in commercial-type diets for fishes are antitrypsin activity in soybeans (Sandholm et al. 1976), mycotoxins in peanut meal and cottonseed meal (Sinnhuber et al. 1977), gossypol in cottonseed meal (Ashley 1972), and cyclopropenoid fatty acids as cocarcinogens fed simultaneously with aflatoxins to rainbow trout (Sinnhuber et al. 1968). An informative review of antinutritional factors in fish feeds is included in a review of nutrient requirements of coldwater fishes (National Research Council 1981).

PROTEIN

Optimal dietary protein concentrations for fish are dictated by a delicate balance of dietary protein-to-energy ratio, plus protein quality (amino acid balance), and nonprotein energy sources (i.e., amount of fat in relation to carbohydrate). Excessive nonprotein energy intake resulting from high digestible energy-to-dietary-protein ratios often causes cessation of feeding before sufficient protein is consumed, since ingestion rate is primarily determined by total available dietary energy content (Page and Andrews 1973). Conversely, slow growth rates may result from low nonprotein energy intake or formula diets may simply be less cost-effective for fish farming purposes. Dietary protein in excess of that required for growth is often utilized for energy in fishes (Cowey 1979). For example, increased gluconeogenesis was demonstrated, as a result of higher activities of the gluconeogenic enzymes, fructose diphosphate, and phosphoenolpyruvate carboxykinase, in rainbow trout fed high dietary protein concentrations (Cowey et al. 1981b). Finally, dietary amino acid imbalances may result in higher dietary protein concentrations than that required for maximal growth as well as antagonisms between some amino acids, such as isoleucine and leucine in chinook salmon, *Oncorhynchus tshawytscha*, (Chance et al. 1964), isoleucine, leucine, and valine in channel catfish (Robinson et al. 1982), or lysine and arginine in salmonids (Rumsey[3]).

---

[3] Gary L. Rumsey, Tunison Laboratory of Fish Nutrition, U.S. Fish and Wildlife Service, Cortland, NY 13045, pers. commun. December 1981.

Since dietary protein quantity and quality are major determinants of growth in fish, numerous investigations have been conducted to determine protein requirements for specific fish species. Protein requirement studies that examine various concentrations of dietary protein with higher carbohydrate concentrations being substituted for protein in lower protein diets often produce reliable approximations of quantitative dietary protein requirements (Table 2). However, according to Rumsey (1978), protein sources generally have higher metabolizable energy values than carbohydrate sources for salmonids. Thus, in many dietary protein requirement studies, fishes were probably offered higher metabolizable energy values in the high protein diets compared with the low protein diets. Since fish fed low protein diets may have had less available energy, additional protein may have been shunted for metabolic requirements other than growth. Many of the quantitative protein requirements, listed in Table 2, may be overestimated values due to this shift in utilization of protein in low protein diets (Rumsey 1978). Therefore, protein-energy studies examining several energy concentrations within each of several dietary protein concentrations provide better estimates of quantitative dietary protein requirements of fishes.

TABLE 2.—Quantitative protein requirements of several fish species.

Species	Initial mean weight	Protein requirement, % dry diet	Study duration (wk)	Rearing temperature (°C)	Criteria[1]	Reference
Salmo gairdneri	6.9	40	10	16-27	G,FC,BP	Satia (1974)
	1.3	45	10	10	G,FC	Halver et al. (1964)
	61.0	42	22	8-12	G,BP	Austreng and Refstie (1979)
	0.7	40	32	15	G,FC	Cho et al. (1976)
	6.5-7.0	[2]40-45	10	9-12.5	G,PER,FC	Zeitoun et al. (1973)
Oncorhynchus kisutch	14.5	40	10	6.5-10.5	G	Zeitoun et al. (1974)
O. tshawytscha	1.5	55	10	15	G	DeLong et al. (1958)
	1.5	40	10	8	G	DeLong et al. (1958)
O. nerka	1.15	45	10	10	G,FC	Halver et al. (1964)
Micropterus salmoides	?	40	2-8	23	G,FC	Anderson et al. (1981)
M. dolomieui	?	45	4-9	20.5	G,FC	Anderson et al. (1981)
Morone saxatilis	2.25	[3]55	6	24.5±2	G,FC	Millikin (1982)
	1.41	47	10	20.5	G,FC	Millikin (in press)
Pleuronectes platessa	14.5	50	12	15	G	Cowey et al. (1972)
Fugu rubripes	2.0	50	3	25-26	G,FC	Kanazawa et al. (1980b)
Anguilla japonica	3.1	44.5	8	25	G,BP	Nose and Arai (1972)
Tilapia zilli	1.65	35	3	24-26	G	Mazid et al. (1979)
T. aurea	0.4	[3]36	12	26-29	G	Davis and Stickney (1978)
Ictalurus punctatus	?	35	26	?	G,FC	Lovell (1972)
	10-25	35	8	28	G,PER	Murray et al. (1977)
Chanos chanos	0.04	40	4	25-28	G,FC	Lim et al. (1979)
Ctenopharyngodon idella	0.15-0.20	41-43	6	22-23	G,PER	Dabrowski (1977)
Cyprinus carpio	5.8	38	4	?	G	Ogino and Saito (1970)
Chrysophrys aurata	2.6	38	16	?	G,FC	Sabaut and Luquet (1973)

[1] G = growth, FC = feed conversion, BP = body protein, PER = protein efficiency ratio.
[2] Protein requirement increased from 40 to 45% as salinity increased from 10 to 20‰.
[3] Highest protein concentration examined.

Dietary protein concentration requirements generally decrease with increasing age or fish size. For example, salmonids require about 50% protein[4] during the initial feeding stage of fry, decreasing to 40% protein after 6 to 8 wk, with a further reduction to 35% protein for yearlings (National Research Council 1973). Channel catfish fry require a minimum of 40% protein, decreasing to 30 to 36% for fingerlings and 25 to 30% protein for subadults weighing >114 g (National Research Council 1977; Andrews 1977). The higher protein concentrations in these two ranges produce better growth of channel catfish fingerlings and subadults, whereas the lower protein concentrations provide better protein conversion (weight protein fed ÷ weight gain) (Andrews 1977).

Increased water temperature has variable effects on the minimal protein or energy requirement for maximal growth rate of fishes. For example, chinook salmon fingerlings require 40% protein at 8°C and 55% protein at 15°C (DeLong et al. 1958). Striped bass fingerlings (initial mean weight = 1.4 g) require 47% protein at 20.5°C, while additional dietary protein is required (about 55%) at 24.5°C for maximal growth of slightly larger fingerlings (initial mean weight = 2.2 g) (Millikin in press and 1982, respectively). In separate studies with rainbow trout fingerlings, 35% dietary protein provided as good a growth rate as 40 or 45% protein within any of several temperature regimes (National Research Council 1981). Fingerlings (mean initial weight = 2.0 g) fed either 35, 40, or 45% protein grew equally well within any one temperature regime (9°, 12°, 15°, and 18°C) over a 16-wk period (Slinger et al. 1977, cited in National Research Council 1981). Slightly larger rainbow trout (mean initial weight = 3.45 g) also grew equally well when fed 35, 40, or 45% dietary protein within any one of three temperature regimes (9°, 12°, or 18°C) over a 24-wk period (Cho and Slinger 1978, cited in National Research Council 1981). Growth rates were progressively higher at each successive increase in rearing temperature, regardless of dietary protein concentration, except for 18°C in the second study. Increased feed consumption of lower protein diets occurred when rainbow trout were reared at higher temperatures and probably satisfied higher protein requirements at elevated water temperatures (National Research Council 1981). Chinook salmon fry (0.4 g) require 53% dietary protein (dry weight basis) combined with 16% dietary lipid (dry weight basis) when reared at 5° or 12°C based upon weight gain and survival rates (Fowler 1980, 1981). However, growth rates were two to three times more rapid for chinook salmon fry reared at 12°C.

---

[4] Nutrient content of diets is expressed as percentage of the diet on a dry weight basis, unless otherwise noted.

Changes in salinity may alter protein requirements of anadromous or euryhaline species. Rainbow trout fingerlings require 45% protein for optimal growth at 20‰ compared with a 40% protein requirement at 10‰ (Zeitoun et al. 1973). Since a salinity of 10‰ is almost isotonic with internal fluids (9‰) of rainbow trout fingerlings, the higher dietary protein requirement for rainbow trout reared in a salinity of 20‰ suggests that the higher dietary protein concentration may assist in osmoregulation in a hypertonic external environment for this species (Zeitoun et al. 1973). Conversely, coho salmon, *O. kisutch*, smolts require 40% protein in 10 and 20‰. Although maximum weight gain occurred at 40% protein in both salinities, maximum protein retention occurred at 40% protein in 10‰ and 50% protein at 20‰ (Zeitoun et al. 1974). The authors concluded that the hyperosmotic environment (20‰) did not stress coho salmon smolts in the same manner as previously shown with smaller rainbow trout fingerlings. Also, underyearling rainbow trout (mean weight = 70 g) require more dietary arginine (1.2% of the diet) when reared in freshwater than in those individuals reared in 20‰ (1.0% arginine of the diet) (Kaushik 1977, cited in Poston 1978). Further work is necessary to more firmly establish whether protein requirements change with salinity for specific life stages of various anadromous or catadromous fish species.

AMINO ACIDS

Qualitative and Quantitative Requirements

Examination of qualitative amino acid requirements of fishes has often been based upon growth and feed efficiency in long-term feeding studies. Typically, one of several amino acids is removed singly from a well-defined formula diet which is assumed to be nutritionally complete (i.e., positive control), to determine if significant reduction in weight gain occurs in fish fed the selected, amino acid-deficient diets compared with growth of fish fed the control diet. Thereafter, any group of fish fed a diet determined to be deficient in an amino acid, as indicated by reduced growth and feed efficiency, is separated into two subgroups: One subgroup is retained on the amino acid-deficient diet (control diet minus one amino acid), whereas the other subgroup is fed the control diet. Reduced growth rate or cessation of growth in fish fed the amino acid-deficient test diet versus the control diet is considered to be confirmation of a dietary requirement for the specific amino acid being tested. On the basis of such amino acid feeding studies, several fish species have been found to require the same 10 amino acids (arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine) as essential dietary constituents. Species requiring dietary inclusion of these amino acids include chinook salmon (Halver et al. 1957); rainbow trout (Shanks et al. 1962); sockeye salmon, *O. nerka* (Halver and Shanks 1960); channel catfish (Dupree and Halver 1970); Japanese eel, *Anguilla japonica*, and European eel, *Anguilla anguilla* (Arai et al. 1972b); common carp (Nose et al. 1974); red sea bream, *Chrysophrys major* (Yone 1975); and redbelly tilapia, *Tilapia zilli* (Mazid et al. 1978).

Qualitative amino acid requirements of plaice, *Pleuronectes platessa*, and sole, *Solea solea*, were investigated, using intraperitoneal injections of uniformly labelled - ^{14}C-glucose into individuals of the two fish species (Cowey et al. 1970). Formation of radioactive labelled aspartic acid, glutamic acid, cysteine, serine, glycine, alanine, and proline over a 6-d period implied that sufficient amounts of these amino acids can be produced by underyearling plaice and sole through intermediary metabolism, thus suggesting dietary nonessentiality of those specific amino acids. On the other hand, arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, and valine were not incorporated from (U - ^{14}C) - glucose, thus implying dietary essentiality. Although the authors suggested that metabolic requirements for tyrosine were provided from hydroxylation of ingested phenylalanine, this still needs to be tested. Possible essentiality of tryptophan was not examined, thereby leaving the status of this amino acid unresolved for the plaice and sole.

Quantitative amino acid requirements determined for several fish species are generally based on weight gain, feed efficiency, and sometimes free amino acid plasma levels of individuals fed graded concentrations of a particular amino acid (Table 3). In addition to those values listed in Table 3, coho salmon have been shown to require 2.4% arginine of the dry diet (6.0% of the dietary protein), 0.7% histidine of the dry diet (1.7% of the dietary protein) (Klein and Halver 1970), and 0.2% tryptophan of the dry diet (0.5% of dietary protein) (Halver 1965). Many similarities exist between species in individual quantitative amino acid requirements when expressed as a percent of dietary protein (Table 3).

Amino acid composition of eggs and larval stages for a given species has been shown to be a good guideline for estimating quantitative amino acid requirements of fry and fingerling stages. For example, diets formulated to contain the amino acid composition of Atlantic salmon eggs promoted better growth of Atlantic salmon fingerlings than use of an amino acid pattern based on the National Research Council's (1973) recommendations for salmonids (Ketola 1980). Ketola (1980) also observed the same pattern of accelerated growth in rainbow trout fry fed diets formulated on the basis of egg amino acid composition of that species compared with the National Research Council's (1973) recommendations. In a separate study, rainbow trout fingerlings were fed a diet containing soybean meal as the sole protein source or the same diet supplemented with amino acids (leucine, methionine, lysine, valine, and threonine) to provide a dietary essential amino acid profile similar to rainbow trout eggs. Improved weight gain occurred in rainbow trout fingerlings fed the amino acid supplemented diet, thereby suggesting the similarity between amino acid profiles of rainbow trout eggs and dietary amino acid requirements of rainbow trout fingerlings (Rumsey and Ketola 1975).

Amino Acid Availability

A significant contribution to channel catfish diet formulation recently came from an extensive investigation of true amino acid availability (corrected for metabolic fecal amino acids) and apparent amino acid availability (digestibility) values of various feedstuffs commonly incorporated into commercial catfish diets (Wilson et al.

TABLE 3.—Quantitative dietary amino acid requirements for several fish species.[1]

Amino acid	Channel catfish[2]	Chinook salmon[3]	Japanese eel[4]	Common carp[5]
Arginine	4.3 (1.0)	6.0 (2.4)	4.5 (1.7)	4.2 (1.6)
Histidine	1.5 (0.4)	1.8 (0.7)	2.1 (0.8)	2.1 (0.8)
Isoleucine	2.6 (0.6)	2.2 (0.9)[6]	4.0 (1.5)	2.3 (0.9)
Leucine	3.5 (0.8)	3.9 (1.6)[6]	5.3 (2.0)	3.4 (1.3)
Lysine	5.1 (1.2)	5.0 (2.0)	5.3 (2.0)	5.7 (2.2)
Methionine	2.3 (0.6)[7]	4.0 (1.6)[8]	5.0 (1.9)[8]	3.1 (1.2)[9]
Phenylalanine	5.0 (1.2)[10]	5.1 (2.1)[6,11]	5.8 (2.2)[11]	6.5 (2.5)[11]
Threonine	2.3 (0.5)	2.2 (0.9)	4.0 (1.5)	3.9 (1.5)
Tryptophan	0.5 (0.1)	0.5 (0.2)	1.1 (0.4)	0.8 (0.3)
Valine	3.0 (0.7)	3.2 (1.3)	4.0 (1.5)	3.6 (1.4)

[1] Expressed as percentage of dietary protein with requirement as percentage of dry diet in parentheses.
[2] Based upon 24% dietary protein (Robinson et al. 1980a).
[3] Based upon 40% dietary protein unless otherwise noted (National Research Council 1973).
[4] Based upon 37.7% dietary protein (Nose and Arai Unpubl. data, cited in Cowey and Sargent 1979).
[5] Based upon 38.5% dietary protein (Nose 1979).
[6] Based upon 41% dietary protein (National Research Council 1973).
[7] In the absence of cystine which can replace 50 to 60% of methionine requirement (Harding et al. 1977).
[8] Methionine + cystine.
[9] In the absence of cystine.
[10] Phenylalanine + tyrosine requirement. Tyrosine can replace ca. 50% of phenylalanine (Robinson et al. 1980a).
[11] In the absence of tyrosine.

1981). Results generally suggested that reasonable agreement occurs between average apparent amino acid availability and protein digestibility values of any one specific protein source. However, individual amino acid availabilities were quite variable within and among various feed ingredients tested. Also, apparent amino acid availability values were considerably less than true amino acid availability values for feed ingredients containing relatively low protein content (e.g., 9 to 19%), such as rice bran, rice mill feed, wheat middlings, and corn.

Lysine

Dietary lysine requirements for fishes range from 5.0 to 6.8% of the dietary protein. In addition to the quantitative lysine requirements listed in Table 3, rainbow trout fry require 6.8% lysine and lake trout, *Salvelinus namaycush*, fry require 6.0% lysine as a percentage of total dietary protein (Ketola 1980). Robinson et al. (1980b) reported a dietary lysine requirement of 5% of the dietary protein for channel catfish fed an adequate dietary protein concentration (30%); thus confirming a dietary lysine requirement (5.1% of the dietary protein) for channel catfish fed a marginal dietary protein concentration of 24% (Wilson et al. 1977). Excessive dietary lysine in the presence of marginal or adequate dietary arginine concentrations did not depress growth or feed efficiency of channel catfish, nor did excessive arginine depress growth or feed efficiency of channel catfish in the presence of marginal dietary lysine concentrations (Robinson et al. 1981). This is in contrast to lysine-arginine antagonisms reported for several terrestrial species (Maynard and Loosli 1969).

Lysine deficiency in fish may conceivably result in depressed rates of collagen formation. Hydroxylysine has been shown to be a constituent of collagen in several fish species (Mehrle[5]). Fin rot occurred in rainbow trout fed a lysine-deficient diet containing corn gluten meal as the sole protein source (Ketola 1979a). Supplementation of a combination of lysine, arginine, histidine, isoleucine, threonine, tryptophan, and valine to the corn gluten meal diet resulted in improved survival, increased growth, and prevention of severe caudal fin erosion. At the same time, removal of lysine from the amino acid mixture in the corn gluten meal supplemented diet increased mortality, reduced growth, and resulted in caudal fin erosion of rainbow trout.

Methionine

Quantitative dietary methionine requirements for several fish species have been shown to depend upon dietary cystine concentration, since cystine can substitute for a portion of the methionine requirement. This is the result of the conversion of methionine to cystine being a common pathway of intermediary metabolism in many terrestrial animals (Maynard and Loosli 1969) as well as fish (National Research Council 1973). Rainbow trout fingerlings require 0.6% methionine (1.7% of the dietary protein) and 0.45% cystine (1.29% of the dietary protein), a total sulfur amino acid requirement of 1.05% of the diet (2.99% of dietary protein). This is based upon growth and feed efficiency as demonstrated by feeding studies, using a factorial design of 0.3 to 0.75% methionine and 0.04 to 0.6% cystine (Page 1978). Excessive cystine for rainbow trout (e.g., 0.6%) did not partially satisfy methionine requirements in methionine-deficient diets (0.3 and 0.45% methionine) based on weight gain and feed conversion. Chinook salmon require 0.5 to 0.6% dietary methionine (1.3 to 1.5% of the dietary protein) in the presence of 1.0% dietary cystine, whereas 1.6% methionine did not produce maximum growth in the presence of 0.05% dietary cystine (Halver et al. 1959). Channel catfish require 0.56% dietary methionine (2.34% of the dietary protein) in the absence of cystine, while 60% of the methionine requirement is replaceable with cystine (Harding et al. 1977).

Methionine deficiency has been shown to result in cataractogenesis in lake trout fingerlings and rainbow trout fingerlings. After 12 wk, rainbow trout fingerlings (initial mean weight = 1.5 g) fed 0.6% methionine plus 0.3 or 0.45% cystine did not develop any cataracts (Page 1978). Lower dietary methionine content (0.3 or 0.45%) combined with dietary cystine content ranging from 0.04 to 0.6% produced varying degrees of cataracts in rainbow trout. In another study, lake trout fingerlings were fed methionine-deficient diets (0.36% methionine = 0.96% of the dietary protein) containing soybean protein isolate as the sole protein source (40% of the diet). After 8 wk, lake trout fingerlings showed only initial signs of opacification of subcapsular areas (Poston et al. 1977). However, after 16 wk, 100% of lake trout fed 0.36% dietary methionine developed bilateral lenticular cataracts, while none of the individuals fed the control diet containing 1.2% dietary methionine (3.27% of the dietary protein) had cataracts.

---

[5] Paul M. Mehrle, Columbia National Fisheries Research Laboratory, U.S. Fish and Wildlife Service, Columbia, MO 65201, pers. commun. December 1981.

Attempts to supplement suboptimal dietary concentrations of methionine plus cystine with dietary taurine or inorganic sulfate have proven unsuccessful with channel catfish fingerlings and rainbow trout fingerlings. Channel catfish fingerlings fed dietary taurine or inorganic sulfate as a partial replacement for methionine had reduced growth rates (Robinson et al. 1978), whereas rainbow trout fingerlings had reduced growth and developed cataractogenesis (Page et al. 1978). The absence of cataractogenesis in methionine-deficient channel catfish may be the result of the relatively shorter duration of this study (8 wk) compared with a 16-wk study on lake trout (Poston et al. 1977). Another explanation for the absence of cataract formation in channel catfish may be due to the slightly larger initial size of channel catfish (mean weight = 7.7 g) compared with lake trout (mean weight = 5 g). Either of these factors may have produced a slower turnover rate of amino acids in channel catfish.

According to a summary by Poston et al. (1977), insufficient methionine often results in reductions in sulfhydryl group concentrations, and lens glutathione synthesis also decreases rapidly during formation of most cataracts. The authors speculated that lens glutathione possibly protects the lens sulfhydryl groups from oxidation.

Tryptophan

Tryptophan deficiency symptoms have been described in rainbow trout; sockeye salmon; brook trout, *S. fontinalis*; and channel catfish. Tryptophan deficiency in rainbow trout and sockeye salmon has resulted in scoliosis (Shanks et al. 1962; Halver and Shanks 1960, respectively). In a separate study with rainbow trout, hyperemia, scoliosis, and abnormal deposition of calcium occurred in kidney and bony plates surrounding the notochord and sheath of fish fed tryptophan-deficient diets (Kloppel and Post 1975). The authors suggested that hyperemia might be attributed to a lack of serotonin resulting from a deficiency of its precursor, tryptophan. In discussing scoliosis, Kloppel and Post (1975) noted that tryptophan is a major component of protocollagen, a supposed precursor of collagen. However, the absence of scoliosis in channel catfish fingerlings fed tryptophan-deficient diets (Wilson et al. 1978), compared with studies on salmonids, probably resulted from a slower growth rate of channel catfish because of a larger initial mean weight (12.5 g).

Quantitative tryptophan requirements have been shown to be similar for three different salmonid species and channel catfish. Almquist-type plots of growth responses indicated dietary tryptophan requirements of 0.15 to 0.25% of the diet (0.4 to 0.6% of dietary protein) for chinook salmon and 0.20 to 0.25% of the diet (0.5 to 0.6% of dietary protein) for sockeye salmon and coho salmon (Halver 1965). Channel catfish fingerlings fed a tryptophan-deficient diet (0.05%) for 8 wk had significantly poorer weight gain and feed efficiency than individuals fed diets containing as low as 0.12% tryptophan (0.5% of dietary protein) (Wilson et al. 1978). Wilson et al. (1978) suggested that the lower dietary tryptophan requirement of fishes compared with that of terrestrial animals may be due to an inability of fish to convert tryptophan to niacin, thus reducing the metabolic need of tryptophan in fishes as compared with terrestrial species. Growth rate of brook trout and the low ratio of two enzyme activities (3-hydroxyanthranilic acid oxygenase to picolinic acid carboxylase) concerned with an intermediate of the conversion pathway of tryptophan to niacin indicated that dietary tryptophan is not an efficient niacin precursor for this species (Poston and DiLorenzo 1973). Additionally, a low ratio of the two liver enzyme activities exists in lake trout, rainbow trout, Atlantic salmon, and coho salmon compared with terrestrial vertebrates (Poston and Combs 1980).

LIPIDS

Optimal Dietary Lipid Concentrations and Protein-to-Energy Ratios

Optimal dietary lipid concentrations for inclusion in formulated feeds for fishes involve consideration of several factors. The minimal dietary lipid concentration that maximizes dietary protein available for growth rather than energy (i.e., protein sparing) may be excessive for diet incorporation if fish are being cultured as a lean product for human consumption, or if freezer storage space is unavailable to retard development of oxidative rancidity of the diets. However, if fish are being hatchery cultured for release into natural waters, high body lipid composition may be beneficial as an energy source during acclimation to natural food (Wedemeyer et al. 1980). Also, feeds that contain the minimal dietary lipid concentration required for maximal protein sparing action for a particular species are relatively cost-effective.

Protein sparing action of various dietary lipid concentrations has been examined for several fish species. Channel catfish fingerlings (mean initial weight = 1.25 g) cultured at 26.7° to 32.2°C and fed 35% protein diets grew faster on 8% dietary lipid, either as beef tallow or corn oil, than on 4% of either dietary lipid source (Dupree 1969a). Dietary lipid concentrations of 16% corn oil or beef tallow reduced growth rate and protein deposition of channel catfish compared with 8% dietary lipid. Therefore, maximal protein sparing action occurred at <16% of either dietary lipid source but ≥8% dietary lipid. In a separate study, larger channel catfish fingerlings (initial mean weight = 7.0 to 7.5 g), cultured at 30°C and fed 25% protein diets containing either 5, 8, 12, 15, or 20% bleached menhaden oil, had maximal weight gain and protein deposition when fed 25% protein with 15% lipid (Dupree et al. 1979). Channel catfish fingerlings (either 0.5 or 1.0 g initial mean weight in separate experiments) reared at 28°C grew faster when fed 35% protein plus 12% lipid, rather than 5% lipid combined with 25 or 35% protein or 12% lipid combined with 25% protein (Murray et al. 1977). Conversely, when channel catfish reared at 23°C were fed 25 or 35% protein combined with 5 or 12% lipid, 5% lipid plus 25 or 35% protein was sufficient for maximal weight gain and food conversion, probably due to lower metabolic requirements. Channel catfish with initial and final mean weights of 14 and 100 g, respectively, required 35% protein and 12% lipid, whereas subadults weighing 114 to 500 g required 25% protein and 12% lipid when reared at 27°C (Page and Andrews 1973). Protein-to-energy ratio requirements of channel catfish fingerlings (initial mean weight = 7.0 g) as a function of protein deposition were found to be 88 mg protein/kcal between dietary energy concentrations of 275 to 341 kcal/100 g when reared at 26.7°C (Garling and Wilson 1976). However, maximal weight gain occurred in fish fed 32 to 36% protein. Therefore, for the most cost-effective feed, the optimal dietary protein concentration for channel catfish fingerlings reared at 26.7°C is between 24 and 32%, when considering weight gain, feed efficiency, and protein deposition. Rainbow trout fingerlings (initial mean weight = 4.8 g) reared at 12.2°C over an 18-wk period had equally good growth rates when fed 35% protein and 24% lipid as individuals fed 44 or 53% protein, each combined with either 8, 16, or 24% lipid. This indicated a minimal dietary lipid concentration of 24% for maximal protein sparing action and an optimal protein-to-energy ratio of 73 mg protein/kcal (Lee and Putnam 1973). Conversely, a study evaluating three dietary protein concentrations (33, 39, and 44%) combined with 22% lipid in each of three forms (22% herring oil, 14.6% herring oil plus 7.4% lard, or 11% herring oil plus 11% lard) in a 3 × 3 factorial showed that better growth was obtained in rainbow trout fingerlings (initial mean weight = 5.4 g) fed 44% protein and 22% lipid, regardless of the ratio of herring oil to lard when reared at 11.5°C over a 14-wk period (Yu et al. 1977). Protein efficiency ratios and protein retention values were similar, regardless of dietary protein concentration and lipid source combinations fed to rainbow trout fingerlings. The contradictory results of these two studies in the minimal dietary protein required (35% protein plus 24% lipid versus 44% protein plus 22% lipid) for maximal growth of rainbow trout fingerlings can be partially explained by differences in dietary fiber concentrations. A low dietary fiber concentration (6.5%) was incorporated in diets containing 36, 44, or 53% protein plus 24% lipid, whereas a high dietary fiber concentration (22.4%) was incorporated in diets containing 36, 44, or 53% protein plus 8% lipid (Lee and Putnam 1973). However, in the study by Yu et al. (1977), dietary fiber concentrations were held constant at 11.2% in all diets. Therefore, variable dietary fiber concentrations in the first study may have differentially affected amino acid absorption rates or feed utilization. Successive increases in dietary lipid concentration of 7, 11, or 16% in 30% protein diets or 9, 15, or 21% lipid in 40% protein diets resulted in increased weight gain and improved feed conversion of rainbow trout fingerlings (initial mean weight = 2 g) within each dietary protein concentration when reared at 11°C (Reinitz et al. 1978b). Minimal dietary protein and lipid concentration requirements were not determined, since the highest dietary protein (40%) plus lipid (21%) combination that was evaluated also produced maximal growth and optimal feed conversion ratios for rainbow trout fingerlings. A separate study demonstrated that about 35% protein combined with either 23 or 27% dietary lipid provided better growth of rainbow trout fingerlings than 36% dietary protein combined with 14% dietary lipid (Reinitz and Hitzel 1980). However, the two high lipid concentration diets did not produce better growth rates of rainbow trout fingerlings than a 35% protein, 18% lipid diet. C. E. Smith et al. (1979) reported that rainbow trout brood stock fed high energy, high protein diets (16% lipid plus 48% protein or 17% lipid plus 49% protein) produced a greater volume of larger eggs than did fish fed diets low and intermediate in energy and protein (6% lipid plus 36% protein or 9% lipid plus 42% protein). However, considerable variation in protein (i.e., amino acid profiles) and lipid (i.e., fatty acid profiles) sources used between diets in this study makes interpretation of the data difficult. Striped bass fingerlings reared at 20.5°C and fed 37, 47, or 57% protein with 7, 12, or 17% lipid in a 3 × 3 factorial design showed maximal protein sparing action of lipid for growth when fed 12% lipid combined with 47% dietary protein or 17% lipid combined with 57% protein (Millikin in press). Juvenile turbot, *Scophthalmus maximus*, fed 35% protein combined with 3, 6, or 9% lipid plus 9 or 18% carbohydrate attained best growth and feed conversion when fed the diet containing 35% protein, 9% carbohydrate, and 9% lipid (Adron et al. 1976). Possibly, additional dietary lipid would have further spared protein for growth rather than energy. Also, a diet containing 35% protein, 9% carbohydrate, and 9% lipid produced similar growth and feed conversion of turbot when compared with a diet containing 55% protein, 9% carbohydrate, and 3% lipid. Juvenile blue tilapia, *Tilapia aurea*, with initial and final mean weights of 2.5 and 7.5 g, respectively, require about 56% protein and 460 kcal/100 g diet (123 mg protein/kcal) while fish >7.5 g required 34% protein and 320 kcal/100 g diet (109 mg protein/kcal) for maximum growth (Winfree and Stickney 1981).

Essential Fatty Acids

Inclusion of either linolenic acid (18:3ω3) or a more highly unsaturated fatty acid in the ω3 series in the diet of rainbow trout is essential. Rainbow trout fingerlings fed diets containing 1% 18:3ω3 as a supplement to 7.8% corn oil doubled their weight gain compared with individuals fed 10% corn oil as the sole dietary lipid source (Lee et al. 1967). Castell et al. (1972a) determined that 1% 18:3ω3 or ethyl linolenate produced larger rainbow trout than 1% linoleic acid (18:2ω6) or ethyl linoleate. Additionally, 1% 18:3ω3 prevented essential fatty acid deficiency symptoms (e.g., fin erosion, heart myopathy, shock syndrome, and swollen, pale livers), while as much as 5% 18:2ω6 did not cure such symptoms (Castell et al. 1972b). Dietary linolenic acid's essentiality and growth enhancing ability for rainbow trout was confirmed in another study, wherein 1% methyl linolenate plus 4% methyl laurate (C 12:0) provided maximal growth and prevention of fatty acid deficiency symptoms compared with fish fed 5% methyl laurate (Watanabe et al. 1974). Rainbow trout fingerlings fed either 0.5% 20:5ω3 or 0.5% 22:6ω3 had better growth rates than individuals fed 0.5% 18:3ω3 in diets containing 5% total lipid, thereby showing a higher essential fatty acid efficiency of 20:5ω3 and 22:6ω3 at low dietary concentrations of these fatty acids (Takeuchi and Watanabe 1977). However, it is unknown whether evaluation of higher dietary concentrations (e.g., 1 to 3%) of each of these fatty acids would have produced similar differences in essential fatty acid efficiencies in terms of growth and feed efficiency of rainbow trout fingerlings. Yu and Sinnhuber (1972) found that 1% dietary 18:3ω3 or 1% docosahexaenoic acid (22:6ω3) provided similar growth rates in rainbow trout fingerlings. No higher dietary concentrations of either fatty acid were studied, nor were total dietary lipid concentrations >2% (dry diet basis) examined. The essentiality of 18:3ω3 for rainbow trout was further substantiated in a 34-mo feeding study in which fingerlings fed 1% ethyl linolenate plus 5% ethyl laurate grew to maturity and produced viable offspring which in turn had normal growth rates (Yu et al. 1979). Incorporation of 1.5% ethyl linoleate to a lipid mix of 1% ethyl linolenate plus 3.5% ethyl laurate did not confer any additional advantage in growth rate, percent fertile eggs, or percent viable fry for rainbow trout compared with individuals fed the 1% ethyl linolenate diet.

Closely related species such as coho salmon and rainbow trout have different quantitative dietary requirements for 18:3ω3 administered as the triacylglycerol, trilinolenin. Coho salmon fingerlings required 1 to 2.5% trilinolenin for maximum growth and feed efficiency when fed dietary trilinolenin concentrations ranging from 0 to 5%. High dietary trilinolein concentrations (>1%) in the presence of the optimal trilinolenin concentrations fed to coho salmon fingerlings resulted in reduced growth rate and feed efficiency values (Yu and Sinnhuber 1979). On the other hand, rainbow trout fingerlings had best growth rates and feed efficiency when fed higher trilinolenin concentrations combined with low trilinolein concentrations (5% trilinolenin plus 0% trilinolein or 3% trilinolenin plus 1% trilinolein) (Yu and Sinnhuber 1976). In a separate study, rainbow trout fingerlings fed a diet sufficient in 18:3ω3 (1% ethyl linolenate) actually had better growth rates and feed efficiency than fish fed 1% ethyl linolenate plus 1.5% ethyl linoleate (Yu and Sinnhuber 1975). Dietary supplements of 5% ethyl linoleate to feeds containing 0.1, 0.5, or 1% ethyl linolenate markedly reduced growth and feed efficiency of rainbow trout fingerlings.

Chum salmon, *O. keta*, fed 5% dietary lipid as either 5% methyl laurate, 4% methyl laurate plus 1% 18:2ω6, 4% methyl laurate plus 1% 18:3ω3, or 3% methyl laurate plus 1% 18:2ω6 and 1% 18:3ω3, showed best weight gain and feed efficiency when offered the 3% methyl laurate plus simultaneous supplements of 1% 18:2ω6 and 1% 18:3ω3 (Takeuchi et al. 1979). Also, simultaneous supplementation of 18:2ω6 (1%) and 18:3ω3 (1%) produced slightly better weight gain of chum salmon fingerlings than 4% methyl laurate plus 1% of a highly unsaturated fatty acid mix (containing 26.5% 20:5ω3 plus 42.1% 22:6ω3). However, minimal dietary requirements of 18:2ω6 or 18:3ω3 for optimal growth rate of chum salmon fingerlings were not determined.

Dietary supplements of either methyl linoleate or methyl linolenate at 0.5 or 1.0% concentrations provided better growth of Japanese eel fingerlings than a fat-free diet or 7% methyl laurate (T. Takeuchi et al. 1980). However, contradictory results in two separate studies by these investigators prevent any conclusions regarding minimal requirements of 18:2ω6 and 18:3ω3 for this species.

Common carp fry and fingerlings have demonstrated better growth when fed diets containing highly polyunsaturated fats (e.g., cod liver oil) than those containing 5% methyl laurate (Watanabe 1975a, b). Intermediate growth rates occurred in common carp fry fed either 1% methyl linoleate or 1% methyl linolenate plus 4% methyl laurate over a 22-wk period (Watanabe et al. 1975a), whereas 1% methyl linoleate or 1% methyl linolenate did not improve growth of common carp fingerlings over an 18-wk period (Watanabe et al. 1975b).

High variability exists among various fish species in ability to elongate and desaturate dietary 18-carbon fatty acids to 20- or 22-carbon fatty acids. Several marine species appear to have lower enzymatic elongation-desaturation capabilities than freshwater fishes. Administration of (1 − ^{14}C) 18:3ω3 to individuals of red sea bream; black sea bream, *Mylio macrocephalus*; opaleye, *Girella nigricans*; striped mullet, *Mugil cephalus*; and rainbow trout indicated that only rainbow trout exhibited appreciable radioactivity in 22:6ω3 of body lipids (Yamada et al. 1980). Therefore, it was concluded that marine species have limited ability to elongate and desaturate 18:3ω3, resulting in dietary essentiality of eicosapentaenoic acid (20:5ω3) or 22:6ω3 and nonessentiality of 18:3ω3. In another study, injections of (1 − ^{14}C) 18:3ω3 into two individuals of each of several fish species resulted in intensive incorporation of 18:3ω3 into 20:5ω3 and 22:6ω3 in rainbow trout, while very low percent bioconversion of 18:3ω3 to 20:5ω3 and 22:6ω3 occurred in marine fish such as globefish, *Fugu rubripes rubripes*; Japanese eel; red sea bream; rockfish, *Sebasticus marmoratus*; and ayu, *Plecoglossus altivelis* (Kanazawa et al. 1979). The results of this study confirmed that pathways of elongation and desaturation of dietary 18-carbon fatty acids are poorly developed in marine fishes compared with rainbow trout. Earlier, Castell et al. (1972c) had reported elevated 20:4ω6 and 22:5ω6 concentrations in body lipids of rainbow trout fed 1% 18:2ω6 as well as elevated 22:6ω3 concentrations in individuals fed 1% 18:3ω3, suggesting an ability of rainbow trout to elongate and desaturate linoleic and linolenic acid. Also, rainbow trout, fed a fat-free diet or 5% oleic acid (18:1ω9) as the sole dietary lipid, accumulated high body lipid concentrations of eicosatrienoic acid (20:3ω9), an indicator of essential fatty acid deficiency in terrestrial animals. Furthermore, comparison of dietary fatty acid composition and initial and final body fatty acid composition of rainbow trout in another feeding study, suggests the ability of this species to elongate and desaturate 20:5ω3 into 22:6ω3 (Castledine and Buckley 1980). Cowey et al. (1976) concluded that turbot lack the necessary microsomal desaturases to effectively convert 18:1ω9, 18:2ω6, or 18:3ω3 into polyunsaturated fatty acids for deposition in neutral fats or phospholipids based upon growth and body lipid composition. Also, 1% dietary 18:3ω3 or 1% arachidonic acid (20:4ω6) in the presence of 4% 18:1ω9 promoted better growth of turbot than 1% 18:2ω6 plus 4% 18:1ω9. Additionally, 1% cod liver oil plus 4% 18:1ω9 produced better growth rates of turbot than all other dietary treatments (Cowey et al. 1976). Simultaneous supplementation of 0.45% 18:2ω6 and 0.45% 18:3ω3 as the only dietary constituents of the ω6 and ω3 series did not increase the level of 20:5ω3 or 22:6ω3 liver triglycerides in underyearling plaice (Owen et al. 1972). Growth studies of red sea bream indicated that a 2% dietary polyunsaturated fatty acid mix (38% 20:5ω3, 1.4% 22:5ω6, and 33.4% 22:6ω3) promoted significantly better weight gain than fish fed up to 4.2% dietary methyl linolenate (Fujii and Yone 1976). It was concluded that 18:3ω3 is not essential for red sea bream, since this species has little, if any, capability to elongate and desaturate 18-carbon fatty acids to 20- and 22-carbon fatty acids, based upon body fatty acid composition.

Specific qualitative and quantitative essential fatty acid requirements have not been determined for channel catfish fry (Yingst and Stickney 1979) and channel catfish fingerlings (National Research Council 1977; Stickney 1977). Nevertheless, growth rates of channel catfish in several studies comparing various lipid sources (e.g., beef tallow, menhaden oil, safflower oil, and corn oil) have consistently been high in individuals fed menhaden oil as the chief dietary lipid (Stickney and Andrews 1971, 1972; Murray et al. 1977; Dupree et al. 1979; Yingst and Stickney 1979, 1980). Typically, menhaden oil contains a large amount of fatty acids of the ω3 family (Stickney 1977), especially the polyunsaturated fatty acids (e.g., 3% 18:3ω3, 17% 20:5ω3, and 13% 22:6ω3). Therefore, ω3 fatty acids may be essential for channel catfish, especially in the fry and early fingerling stages.

Unlike most fish species studied, *Tilapia zilli*, fingerlings require 1% 18:2ω6 or 20:4ω6 for optimal weight gain as opposed to fatty acids of the ω3 series (Kanazawa et al. 1980a). However, this same species has a greater relative ability to elongate and desaturate 18:3ω3 to 20:5ω3 and 22:6ω3, than to elongate and desaturate 18:2ω6 to 20:4ω6 (Kanazawa, Teshima, and Imai 1980).

In a review of lipid requirements of fishes, Castell (1979) discussed differences in fatty acid composition of fishes due to salinity, temperature, diet composition, depth, seasonal variation, and reproductive stage; requirements, metabolism, and functions of dietary fatty acids for fishes are also discussed.

CARBOHYDRATES

Carbohydrates are included in formulated feeds for fish primarily as a low cost source of energy to spare dietary protein for growth rather than energy. Protein sparing action of dietary carbohydrate was demonstrated in brook trout fed marginal concentrations of dietary protein (28 or 32%) with optimal protein-to-calorie ratios of 75 mg protein/kcal (Ringrose 1971).

Maximal dietary carbohydrate concentrations that can be fed to fish without reducing growth rate depend upon whether the fish species is carnivorous, omnivorous, or herbivorous. For example, maximal dietary dextrin concentrations that did not reduce growth rate were 10% for yellowtail, *Seriola quinqueradiata*, 20% for red sea bream and 30% for common carp (Furuichi and Yone 1980). Rainbow trout subadults can be fed 38% wheat meal or 41% cooked wheat (17 to 25% of dietary metabolizable energy) without deleterious effects on growth (Edwards et al. 1977). Similarly, rainbow trout fed 32% wheat meal or 21% wheat meal plus 13% glucose (15 and 26% metabolizable energy of the diet) did not have significant differences in growth rate (Refstie and Austreng 1981). However, dietary Cerelose[6] concentrations as low as 14%, substantially increased liver glycogen concentrations of rainbow trout compared with fish fed 0 or 7% dietary Cerelose (Hilton 1982). Additionally, low rearing temperatures (10° vs. 15°C) for rainbow trout resulted in increased liver glycogen concentrations. Therefore, Hilton (1982) suggested that stocking rainbow trout with high liver glycogen concentrations into natural waters could result in impaired liver function. Incipient lethal levels of waterborne copper were reported to be lower for rainbow trout fed higher concentrations of available carbohydrate, probably as the result of impaired liver function from high liver glycogen content (Dixon and Hilton 1981).

Digestibility of carbohydrates is generally inversely related to molecular complexity. Thus, monosaccharides are more available nutritionally to fishes than are disaccharides, which in turn are more available than are polysaccharides. Relative growth rates of chinook salmon fingerlings fed 20% carbohydrate were as follows: glucose > sucrose > fructose > maltose > dextrin > potato starch > galactose (Buhler and

---

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Halver 1961). Brook trout fingerlings (initial mean weight = 1.6 g) fed 14% glucose, galactose, or fructose over a 20-wk period had better growth rates when fed 14% glucose or fructose (McCartney 1971). Rainbow trout fingerlings had better growth rate, feed conversion, and protein efficiency when fed 30% glucose concentrations compared with 30% raw corn starch or 15% glucose plus 15% cellulose (Bergot 1979a). Dietary glucose concentrations as high as 30% doubled plasma glucose 6 h after the first meal, while normal plasma glucose concentrations were attained 24 h later (Bergot 1979b). Channel catfish fingerlings can utilize 2.25 g of dextrin in place of 1 g of lipid for growth equally well within dietary lipid concentrations of 5 to 12.5% and digestible carbohydrate concentrations of 5.6 to 22.5% (Garling and Wilson 1977).

Dietary fiber is not required by fishes and is considered to be a nonnutrient bulk component in fish diets. According to Leary and Lovell (1975), dietary cellulose in excessive amounts probably decreases absorption of essential nutrients by physical obstruction of enzymes and increased rate of passage through the digestive system. Obstruction of enzyme activity may result from ingested fiber chelating metal ions serving as cofactors of enzymes. Dietary cellulose concentrations as high as 8% did not inhibit growth of channel catfish, whereas 14% dietary cellulose depressed growth. No similar studies have been conducted with salmonids or other fish species to evaluate maximum tolerable, dietary fiber concentrations.

Cellulase activity in stomachs of several fish species and intestinal portions of stomachless Cyprinidae was positively correlated with amount of detritus consumed (Prejs and Blaszczyk 1977). Microflora ingested along with detrital material is probably responsible for the cellulase activity in fish; however, further research should examine sources of cellulase activity, especially in herbivorous species.

VITAMINS

Qualitative vitamin requirements of fishes (National Research Council 1973, 1977) and their biochemical and physiological functions are generally similar to requirements and functions demonstrated for terrestrial animals. Early qualitative vitamin requirement studies of fishes usually consisted of long-term feeding trials (e.g., 14 to 24 wk) in which laboratory cultured salmonids were fed a positive control diet (i.e., assumed to be nutritionally complete) or that same diet omitting one of several vitamins (McLaren et al. 1947; Halver and Coates 1957; Coates and Halver 1958). Growth, survival, behavior, internal organ appearance, blood physiology, and histopathology were often examined to describe deficiency symptoms. Also, fish fed a vitamin-deficient diet were often divided into two subgroups during the course of the study. One subgroup remained on the vitamin-deficient diet while the recovery subgroup was fed the complete diet to detect positive responses such as accelerated growth rate and disappearance of deficiency symptoms.

More recently, biochemical criteria such as activities of specific enzymes requiring a given vitamin for coenzyme formation have been used to determine qualitative and quantitative vitamin requirements of fishes (C. E. Smith et al. 1974; Cowey 1976). According to C. E. Smith et al. (1974), biochemical defects in the form of reduced enzyme activity allow detection of preclinical vitamin deficiencies. A review of vitamin requirements of fishes was presented by Halver (1979).

Thiamine

Essentiality of dietary thiamine has been verified for brook, brown (*Salmo trutta*), and rainbow trout (McLaren et al. 1947; Phillips and Brockway 1957), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967a; Aoe et al. 1969), Japanese eel (Arai et al. 1972a), red sea bream (Yone 1975), and turbot (Cowey et al. 1975). Thiamine deficiency symptoms commonly observed in many of these fish species include anorexia, poor growth, depigmentation, and loss of equilibrium. Hemorrhage and congestion of fins has been noted in thiamine-deficient Japanese eel (Hashimoto et al. 1970; Arai et al. 1972a) and thiamine-deficient common carp (Aoe et al. 1969).

Quantitative thiamine requirements have been determined for turbot and channel catfish. Cowey et al. (1975) detected optimal erythrocyte transketolase (thiamine pyrophosphate serves as coenzyme) activity in turbot fed 2.6 mg thiamine/kg dry diet, whereas maximal growth occurred at dietary thiamine concentrations ≥0.6 mg/kg dry diet. Therefore, in addition to growth rates, functional evidence such as enzyme activity also provides additional useful information for estimating quantitative vitamin requirements. Channel catfish fingerlings require a minimal dietary thiamine concentration of 1 mg/kg dry diet based upon maximal weight gain, feed efficiency, and prevention of thiamine deficiency symptoms such as anorexia, poor growth, dark coloration, and higher mortality (Murai and Andrews 1978a). Hematocrit values of channel catfish were unaffected by dietary thiamine concentrations ranging from 0.1 to 20.1 mg/kg dry diet.

It is unknown why channel catfish and common carp require lower dietary concentrations of thiamine compared with salmonids. Omnivorous fish would seemingly require higher amounts of thiamine for oxidative decarboxylation of pyruvate and the transketolase reaction of the pentose phosphate shunt, due to the ability of herbivores and omnivores to metabolize higher dietary carbohydrate concentrations than carnivorous fish such as salmonids (Murai and Andrews 1978a).

Riboflavin

Dietary essentiality for riboflavin has been reported for rainbow trout (McLaren et al. 1947), brook, brown, and lake trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), Atlantic salmon (Phillips 1959a), channel catfish (Dupree 1966), common carp (Aoe et al. 1967a; Ogino 1967), rainbow trout (Kitamura et al. 1967a; Poston et al. 1977; L. Takeuchi et al. 1980), Japanese eel (Arai et al. 1972a), and red sea bream (Yone 1975). Rainbow trout (mean initial weight = 5.9 g) fed riboflavin-deficient diets developed bilateral corneal and lenticular lesions after 11 and 15 wk of the experimental period (Poston et al. 1977). Further evaluations of cataract formations induced from riboflavin deficiency in rainbow trout fingerlings confirmed no retinal damage according to histopathological examinations (Hughes et al. 1981a). Fin necrosis, snout erosion, and spinal deformation also occurred in riboflavin-deficient rainbow trout (Poston et al. 1977). In a separate study, rainbow trout fingerlings (initial mean weight = 1.5 g) fed riboflavin-deficient diets displayed anorexia, poor growth, high mortality rate, lesion of fins, and cataract formation during an 8-wk study (L. Takeuchi et al. 1980). Common carp fingerlings fed riboflavin-deficient diets showed anorexia, poor growth, high mortality rate, and hemorrhage of skin and fins (L. Takeuchi et al. 1980). Murai and Andrews (1978b) reported 100% occurrence of "short body dwarfism" due to shortening of individual vertebrae in riboflavin-deficient channel catfish after 20 wk. These authors speculated that abnormal vertebral growth may be related to hypothyroidism which in turn may be caused by riboflavin deficiency.

Quantitative riboflavin requirements have been determined for common carp, rainbow trout, and channel catfish. In several different studies, riboflavin requirements of carp fingerlings apparently declined with increasing fish size based on growth rate and liver riboflavin content. Common carp fingerlings with an initial mean weight equalling 1.5 g required 20 mg riboflavin/kg dry diet over a 6-wk period (Aoe et al. 1967a). Slightly larger carp fingerlings (initial mean weight = 2.8 g) required 10 mg riboflavin/kg dry diet over a 6-wk period (Ogino 1967), whereas individuals with an initial mean weight equalling 3.4 g required 5 to 7 mg riboflavin/kg dry diet (L. Takeuchi et al. 1980). Rainbow trout with an initial mean weight of 7 g required 12.2 mg riboflavin/kg for maximal growth, whereas 18.2 mg riboflavin/kg were required for saturation of head and posterior kidney tissue (Woodward 1982). However, larger rainbow trout fingerlings (initial mean weight = 11.2 g) required 3 mg riboflavin/kg dry diet according to growth, food conversion, and mean erythrocyte glutathione reductase activity coefficient or 12 mg riboflavin/kg dry diet for maximal liver riboflavin content (Hughes et al. 1981b). Rainbow trout fingerlings (initial mean weight = 1.5 g) required 4 mg riboflavin/kg dry diet based upon growth rate and feed efficiency and 6 mg riboflavin/kg dry diet based on liver riboflavin content (L. Takeuchi et al. 1980). Channel catfish fingerlings require 9 mg riboflavin/kg dry diet for maximal growth and 3 mg riboflavin/kg dry diet to prevent occurrence of short body dwarfism (Murai and Andrews 1978b).

Pyridoxine

Dietary essentiality of pyridoxine has been reported for rainbow trout (McLaren et al. 1947), brook, brown, and lake trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), Atlantic salmon (Phillips 1959a), coho salmon (Coates and Halver 1958), common carp (Ogino 1965), channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967a), yellowtail (Sakaguchi et al. 1969), Japanese eel (Arai et al. 1972a), red sea bream (Yone 1975), turbot (Adron et al. 1978), and gilthead bream, *Sparus aurata* (Kissil et al. 1981). Coates and Halver (1958) mentioned several pyridoxine deficiency symptoms for coho salmon including nervous disorders, hyperirritability, poor appetite, indifference to light, and rapid occurrence of postmortem rigor mortis. Halver (1957) reported the following additional pyridoxine deficiency symptoms for chinook salmon: ataxia, edema of peritoneal cavity, colorless serous fluid, blue-green coloration on dorsal surface, and excessive flexing of opercles. Clinical signs of pyridoxine deficiency in rainbow trout include hyperirritability, nervous disorders, erratic and rapid swimming, flexing of opercles, greenish-blue coloration, and tetany, just before death (C. E. Smith et al. 1974). Pyridoxine-deficient rainbow trout displayed normocytic, normochromic anemia, indicating that pyridoxine has a function in maintenance of normal erythropoiesis in this species (C. E. Smith et al. 1974). Also, rainbow trout fed pyridoxine-deficient diets for 7 d had lower aspartate aminotransferase activity in white muscle, whereas liver aspartate and alanine aminotransferase activity was reduced after 28 d (Jurss 1978, 1981). Pyridoxine deficiency symptoms in channel catfish fingerlings included nervous disorders, erratic swimming, opercle extension, and tetany (Dupree 1966). Andrews and Murai (1979) confirmed a pyridoxine requirement for channel catfish fingerlings, reporting that fish fed pyridoxine-deficient diets displayed anorexia, nervous disorders, tetany, and blue-green coloration on the dorsal surface. No anemia was detected in pyridoxine-deficient individuals, whereas a microcytic, normochromic anemia was observed in channel catfish fed 20 mg/kg or greater of pyridoxine. Chinook salmon fingerlings fed a high protein diet (65%) require about 15 mg pyridoxine/kg diet for optimal growth and disease resistance to *Vibrio anguillarum* (Hardy et al. 1979).

Quantitative pyridoxine requirements are known for channel catfish, red sea bream, gilthead bream, turbot, and common carp. Channel catfish fingerlings require a minimum of 4.2 mg pyridoxine/kg dry diet for maximal growth (Andrews and Murai 1979). Red sea bream required a minimum of 5 to 6 mg pyridoxine/kg dry diet for maximal glutamic oxaloacetic transaminase activity and maximal glutamic pyruvate transaminase activity (Yone 1975). A minimum of 2 to 5 mg pyridoxine/kg dry diet is required for maximal weight gain and pyridoxine liver content of red sea bream (Yone 1975). Kissil et al. (1981) reported optimal dietary pyridoxine concentrations for gilthead bream as a function of growth (1.97 mg pyridoxine/kg dry diet) and liver alanine aminotransferase activity (3.0 to 5.1 mg pyridoxine/kg dry diet). Pyridoxine deficiency symptoms in gilthead bream included hyperirritability, erratic swimming behavior, poor food conversion, retarded growth, and high mortality. Turbot fed pyridoxine concentrations of 1.0 mg/kg dry diet up to 30 mg/kg had similar growth rates, whereas individuals fed 0.26 or 0.50 mg pyridoxine/kg dry diet had reduced weight gain (Adron et al. 1978). Liver alanine aminotransferase activity and muscle and liver aspartate aminotransferase activity increased with higher dietary pyridoxine concentrations up to 2.5 mg/kg dry diet. Therefore, a dietary pyridoxine concentration of 2.5 mg/kg dry diet satisfied both maximal growth and liver aspartate aminotransferase activity for turbot. Common carp fingerlings required 5.4 mg pyridoxine/kg dry diet for maximal growth rate and prevention of deficiency symptoms (Ogino 1965).

Niacin

Niacin has been shown to be an essential dietary constituent for rainbow trout (McLaren et al. 1947), brook and brown trout (Phillips and Brockway 1957), lake trout (Phillips 1959b), chinook salmon (Halver 1957), channel catfish (Dupree 1966), common carp (Aoe et al. 1967c), Japanese eel (Arai et al. 1972a), brook trout (Poston and DiLorenzo 1973), and red sea bream (Yone 1975). Hemorrhage and lesions of the skin have been reported in niacin-deficient channel catfish (Andrews and Murai 1978) and Japanese eel (Arai et al. 1972a). Dietary requirements for maximal growth include 28 mg niacin/kg dry diet for common carp (Aoe et al. 1967c) and 14.4 mg niacin/kg dry diet for channel catfish fingerlings (Andrews and Murai 1978).

Pantothenic Acid

Essentiality of dietary pantothenic acid has been demonstrated for rainbow trout (McLaren et al. 1947), brown, brook, rainbow, and lake trout (Phillips and Brockway 1957), Atlantic salmon (Phillips 1959a), chinook salmon (Halver

1957), coho salmon (Coates and Halver 1958), channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967a), Japanese eel (Arai et al. 1972a), and red sea bream (Yone 1975). Most of these species fed pantothenic acid-deficient diets displayed mucous covered gills, anorexia, reduced weight gain, and "clubbed gills."

Quantitative pantothenic acid requirements have been determined for channel catfish fry (250 mg/kg dry diet) and channel catfish fingerlings (10 mg/kg dry diet) (Murai and Andrews 1975 and 1979, respectively) and common carp fingerlings (40 mg/kg dry diet) (Ogino 1967). Murai and Andrews (1975) suggested that the relatively high dietary pantothenic acid requirements of channel catfish fry might be partially due to higher rates of micronutrient losses in small feed crumbles (high surface to volume ratio) fed to fry compared with larger feed particles fed to fingerlings.

Ascorbic Acid

Ascorbic acid has several important physiological functions in fishes and is the vitamin most sensitive to processing and storage losses in fish formula feeds. Therefore, extensive research has been conducted on qualitative and quantitative ascorbic acid requirements for fishes. Ascorbic acid is a cofactor of an enzyme which is involved in hydroxylation of proline and lysine during collagen formation, thereby contributing to bone and skin formation. Ascorbic acid also has a role in iron metabolism and detoxification of organic pollutants such as toxaphene and polychlorinated biphenyls during accumulation in the liver.

Qualitative dietary ascorbic acid requirements have been reported for rainbow trout (McLaren et al. 1947; Kitamura et al. 1965; Hilton et al. 1978; Sato et al. 1978; John et al. 1979), brook trout (Poston 1967), coho salmon and rainbow trout (Halver et al. 1969), yellowtail (Sakaguchi et al. 1969), Japanese eel (Arai et al. 1972a), channel catfish (Lovell 1973; Wilson and Poe 1973), red sea bream (Yone 1975), mrigal, *Cirrhina mrigala* (Mahajan and Agrawal 1980a), and snake head, *Channa punctatus* (Mahajan and Agrawal 1979). Ascorbic acid deficiency symptoms in coho salmon and rainbow trout include reduced growth, distorted and twisted filament cartilage of the gill arches, acute lordosis and scoliosis, and eventual dislocation of vertebrae (Halver et al. 1969). Other physiological changes in ascorbic acid-deficient rainbow trout include low hematocrit values (Hilton et al. 1978; John et al. 1979), and high plasma levels of triglycerides and cholesterol (John et al. 1979). Halver (1972b) reported that the rate of repair of experimentally induced wounds in salmonids is directly related to the amount of ascorbic acid intake. Rainbow trout fed ascorbic acid-deficient diets for 18 wk displayed impaired collagen formation in the skin according to an in vitro radioisotopic method with labeled proline (Yoshinaka et al. 1978). Brook trout fingerlings fed ascorbic acid-deficient diets over a 34-wk period developed scoliosis and/or lordosis, increased mortality rate, and internal hemorrhaging (Poston 1967). Scorbutic channel catfish experienced lordosis, scoliosis (and ultimately, broken back), hemorrhage within the vertebral column, and brittle vertebrae (Wilson and Poe 1973). Also, these investigators reported reduced serum alkaline phosphatase activity (65% lower), lower vertebral collagen content (42% less on a dry basis), and less hydroxyproline in the collagen of scorbutic channel catfish. Wilson and Poe (1973) speculated that reduced serum alkaline phosphatase activity may indicate reduced bone formation from lower osteoblastic activity. In addition to the aforementioned common ascorbic acid deficiency symptoms (e.g., lordosis, scoliosis, hemorrhage along spinal column, and poor growth), channel catfish had increased susceptibility to pathogenic bacterial infestation (*Aeromonas liquefaciens*) and occasional formation of hemivertebrae (Lovell 1973). Also, Halver et al. (1975) reported hyperplasia of nuclei of eye support cartilage in salmonids deficient in ascorbic acid. Vertebral collagen percentages of 24.5% or less and liver ascorbic acid concentrations of 50 μg/g or less occurred in ascorbic acid deficient channel catfish fingerlings with an initial mean weight equalling 22 g (Lovell and Lim 1978). In contrast, channel catfish fingerlings fed sufficient ascorbic acid had 26% or greater vertebral collagen and 65 μg or greater ascorbic acid/g of liver tissue. In a separate study, Lim and Lovell (1978) reported the following ascorbic acid deficiency symptoms in smaller channel catfish fingerlings (initial mean weight = 2.3 g): 1) anorexia after 9 wk, 2) scoliosis, lordosis, and darker pigmentation after 10 wk, and 3) lower hematocrit values after 18 wk. Also, liver ascorbic acid concentrations of 30 μg/g and vertebral collagen percentages of 25% or less occurred in ascorbic acid-deficient channel catfish in this smaller size range. Snake heads with ascorbic acid deficiency had an elevated liver cholesterol content after 150 d, in addition to the occurrence of scoliosis, lordosis, and decreased ascorbic acid concentrations in blood and kidney (Mahajan and Agrawal 1979). Ascorbic acid deficiency in fish from the same study resulted in normochromic, normocytic anemia after 120 d and normochromic, macrocytic anemia between 180 and 210 d (Agrawal and Mahajan 1980). Using ^{45}Ca as a tracer, snake heads had reduced absorption of calcium from surrounding water by gills and skin and lower muscle and bone calcium content when fed an ascorbic acid-deficient diet for 210 d (Mahajan and Agrawal 1980b). Since distortion of gill filaments from cartilage malformation often occurs in ascorbic acid-deficent fish, decreased calcium absorption through the gills may have resulted from the ascorbic acid deficiency (Mahajan and Agrawal 1980b). Channel catfish (initial weight slightly >5 g), fed either 670 or 5,000 mg of ascorbic acid/kg dry diet, did not receive any additional advantages in weight gain or backbone collagen concentration (Mayer et al. 1978). However, channel catfish exposed to increasingly higher concentrations of toxaphene were at least partially protected from growth retardation, vertebral development anomalies, and skin integrity problems, when higher dietary ascorbic acid concentrations were consumed. For instance, the no-effect toxaphene concentration on skin integrity (e.g., mucous cell numbers and epidermal thickness) was <37 ng/l for channel catfish fed 63 or 670 mg ascorbic acid/kg dry diet, while the no-effect toxaphene concentration was between 68 and 108 ng/l for fish fed 5,000 mg ascorbic acid/kg dry diet (Mayer et al. 1978). Methods to measure rupture (the force level causing specimen failure) and elastic limit (the force level above which permanent structural damage occurs in a test specimen) according to Hamilton et al. (1981a) were used to evaluate effects of ascorbic acid deficiency on bone strength of channel catfish (Hamilton et al. 1981b). Channel catfish fingerlings (initial weight = 4 to 5 g) fed diets containing no ascorbic acid had significant reductions in length and weight after 150 d. Also, after 150 d, fish fed no supplemental ascorbic acid had reductions of 10% in backbone collagen and 16% in hydroxyproline concentration in collagen. Additionally, in channel catfish fed no supplemental ascorbic acid, 24% less force was required to cause permanent damage of vertebral centra (elastic limit) and failure of vertebral centra (rupture) occurred at 16% less force than in individuals fed 500 mg ascorbic acid/kg dry diet.

Quantitative ascorbic acid requirements have been determined for several fish species. Rainbow trout (initial mean weight = 0.3 g) require 100 mg ascorbic acid/kg dry diet and coho salmon (initial mean weight = 0.4 g) require about 50 mg ascorbic acid/kg dry diet based upon blood and anterior kidney ascorbic acid concentrations and growth rate (Halver et al. 1969). The minimal level of ascorbic acid in the blood of coho salmon and rainbow trout accompanying normal growth and survival rate is 35 μg ascorbic acid/g blood. Hilton et al. (1978) reported a lower ascorbic acid requirement (40 mg/kg dry diet) for larger rainbow trout (initial mean weight = 6.7 g), based upon growth, feed conversion, survival rate, and serum iron levels. Andrews and Murai (1975) estimated that channel catfish fingerlings (initial mean weight = 2.3 g) require 50 mg ascorbic acid/kg dry diet over a 28-wk period based on growth, feed conversion, and absence of ascorbic acid deficiency symptoms. Channel catfish fingerlings (initial mean weight = 2.3 g) required 30 mg ascorbic acid/kg dry diet over a 22-wk period for maximal growth, whereas 60 mg ascorbic acid/kg (the next highest experimental concentration) was sufficient to prevent distortion of gill filament cartilage and promote regeneration of skin and muscle in experimentally inflicted wounds after 10 d (Lim and Lovell 1978). Mahajan and Agrawal (1980a) concluded that mrigal fry and fingerlings require about 700 mg ascorbic acid/kg dry diet based upon growth, survival rates, and percentage occurrence of skeletal deformities.

Several sources of dietary ascorbic acid have been evaluated for relative nutritional value for channel catfish and rainbow trout. Channel catfish fingerlings (initial mean weight = 7.9 g) fed equimolar concentrations of 25 mg L-ascorbic acid (uncoated or ethylcellulose coated) or dipotassium L-ascorbate 2-sulfate dihydrate (AS) per kg dry diet over a 20-wk period did not show scoliosis, whereas 42% of the fingerlings fed a diet containing <5 mg ascorbic acid/kg dry diet had scoliosis (Murai et al. 1978). Maximal weight gains and feed efficiency of channel catfish varied with dietary ascorbic acid sources. Only 50 mg of ethylcellulose coated or uncoated L-ascorbic acid were required for maximal growth and feed efficiency, while 200 mg of L-ascorbate-2-sulfate dihydrate were required for similar increments of weight gain. Generally, growth reached a maximum when blood L-ascorbic acid concentrations reached 7 μg/ml (Murai et al. 1978). Rainbow trout which were considerably younger (0.3 g) than channel catfish from the previous study, required about 80 mg of dipotassium ascorbic-2-sulfate (DAS)/kg dry diet over a 20-wk period to avoid ascorbic acid deficiency symptoms in the majority of fishes, and 160 mg DAS/kg dry diet to achieve normal growth (Halver et al. 1975).

Choline

Dietary essentiality of choline has been demonstrated for rainbow trout (McLaren et al. 1947), brook and brown trout (Phillips and Brockway 1957), lake trout (Phillips 1959b), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967a), common carp (Ogino et al. 1970a), Japanese eel (Arai et al. 1972a), and red sea bream (Yone 1975). Choline deficiency symptoms in fish include poor growth and feed efficiency, anorexia, fatty livers, and hemorrhagic areas in kidneys, liver, and intestine.

Quantitative choline requirements have been estimated for common carp fingerlings and lake trout fingerlings. Ketola (1976) examined relative growth rates of lake trout fed an unsupplemented diet (30 mg choline/kg dry diet) compared with equimolar supplements of aminoethanol, dimethylaminoethanol, methylaminoethanol, betaine·HCl, and choline (equivalent to 2,600 mg choline/kg dry diet). Lake trout fed the unsupplemented diet and aminoethanol and betaine supplements had reduced growth rates and high liver fat content. It was concluded that since betaine, a source of labile methyl groups, did not affect growth or liver fat content, any metabolic function of choline in regulation of liver fat in lake trout is unrelated to transmethylation. In a separate feeding study, a quantitative dietary choline requirement of 1,000 mg/kg dry diet was determined for lake trout fingerlings (Ketola 1976). Common carp require an estimated minimal dietary choline·Cl concentration of 2,000 mg/kg dry diet based upon slightly reduced growth and fatty livers in individuals fed choline-deficient diets (Ogino et al. 1970a). The possible role of methionine as a methyl donor and its relative efficiency in preventing fatty liver and hemorrhagic degenerations of kidneys of choline-deficient fish has not yet been investigated.

Folic Acid and Cyanocobalamin

Qualitative folic acid requirements have been demonstrated for brook, brown, and rainbow trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), channel catfish (Dupree 1966), rainbow trout (McLaren et al. 1947; Kitamura et al. 1967a), Japanese eel (Arai et al. 1972a), and rohu, *Labeo rohita* (John and Mahajan 1979). However, common carp fingerlings (mean initial weight = 2.5 g) fed several folic acid concentrations (0 to 15 mg/kg diet) over 16 wk did not show differential responses in growth, feed conversion, folic acid liver content, and erythrocyte counts (Aoe et al. 1967b).

Folic acid deficiency symptoms in chinook salmon include poor growth, anorexia, anemia, lethargy, dark coloration, and megaloblastic erythropoiesis (Halver 1957), while coho salmon displayed poor growth and anorexia (Coates and Halver 1958). Channel catfish fed folic acid-deficient diets displayed lethargy, anorexia, and increased mortality (Dupree 1966). Anemia in coho salmon fed folic acid-deficient diets was macrocytic with poikilocytosis of erythrocytes and a reduction in number of the erythrocytes (Smith and Halver 1969). Clinical folic acid deficiency symptoms in coho salmon in the same study included reduced growth, pale gills, exophthalmia, dark coloration, and distended abdomens with ascites fluid. These authors suggested that blood cell formation in fish is very sensitive to folic acid deficiency because of the importance of folic acid in incorporation of nucleotides into deoxyribonucleic acid. Phillips (1963) detected anemia (type was not reported) in brook trout fingerlings fed folic acid-deficient diets after 9 wk.

Qualitative cyanocobalamin requirements have been demonstrated for chinook salmon (Halver 1957) and channel catfish (Dupree 1966). Halver (1957) reported growth retardation and reduced hemoglobin concentrations and erythrocyte numbers in chinook salmon fed a cyanocobalamin-deficient diet for 16 wk. Channel catfish fed cyanocobalamin-deficient diets displayed growth retardation after 36 wk (Dupree 1966) or lower hematocrits after 24 wk (Limsuwan and Lovell 1981). Limsuwan and Lovell (1981) demonstrated that intestinal microorganisms synthesized about 1.4 ng of cyanocobalamin/g body weight per day. Lack of differences in growth, hemoglobin concentration, and erythrocyte numbers in fish fed either 21.8 ng cyanocobalamin/g diet or 1.8 ng cyanocobalamin/g diet suggested that cyanocobalamin requirements are marginal for channel catfish (initial mean weight = 7.1 g) over a 24-wk period. However, channel catfish fry and early fingerling stages may have demonstrated a cyanocobalamin requirement under similar conditions.

The effects of feeding folic acid-deficient or folic acid plus vitamin B_{12} (cyanocobalamin)-deficient diets have been examined with brook trout (Phillips 1963) and rohu (John and Mahajan 1979). During the time interval between 9 and 15 wk of a feeding study, anemia was more pronounced in brook trout fed a diet deficient in both vitamin B_{12} and folic acid than in individuals fed a diet deficient in folic acid only. Lethargy, muscular loss, and poor growth rate were accentuated in rohu fed a diet concurrently deficient in folic acid and cyanocobalamin, compared with fish fed diets deficient in either folic acid or cyanocobalamin, singly. Megaloblastic anemia occurred in rohu fed a folic acid-deficient diet, a cyanocobalamin-deficient diet, and a diet deficient in both vitamins (John and Mahajan 1979).

Biotin

Qualitative dietary requirements for biotin have been demonstrated for brook, brown, and lake trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), goldfish, *Carassius auratus* (Tomiyama and Ohba 1967), common carp (Ogino et al. 1970b), Japanese eel (Arai et al. 1972a), channel catfish (Robinson and Lovell 1978), and lake trout (Poston and Page 1982). Biotin deficiency symptoms generally occurring in salmonids include anorexia, poor growth, and depressed liver acetyl CoA carboxylase and pyruvate carboxylase (Poston and Page 1982). Biotin deficiency signs include spastic convulsions, fragmentation of erythrocytes, and muscle atrophy in chinook salmon (Halver 1957), depigmentation in channel catfish (Robinson and Lovell 1978), abnormal synthesis of liver fatty acids and high liver glycogen content in brook trout (Poston and McCartney 1974), pale-colored gills often with a mucous coating, protruding beyond the operculum in rainbow trout (Castledine et al. 1978), and high rates of deposition of glycogen in kidney tubules and short, thick gill lamellae in lake trout (Poston and Page 1982).

Biotin has been shown to be important in affecting growth and acetyl CoA carboxylase activity in fish. Lake trout fingerlings required a minimum of 0.1 mg biotin/kg dry diet for optimal growth rate and a minimum of 0.5 mg biotin/kg dry diet for optimal swimming stamina (Poston 1976a). Acetyl coenzyme A carboxylase activity has been shown to be fully activated in livers of rainbow trout containing >3.3 μg biotin/g liver (Castledine et al. 1978). Dietary biotin concentrations of 8 mg/kg dry diet enhanced liver pyruvate decarboxylase activity in channel catfish fingerlings (Robinson and Lovell 1978), whereas 6 mg biotin/kg dry diet increased acetyl CoA carboxylase and pyruvate decarboxylase activities in brook trout fingerlings (Poston and McCartney 1974). Common carp fingerlings require 1 mg biotin/kg dry diet for maximal weight gain and biotin liver content (Ogino et al. 1970b).

Since biotin-containing lipogenic and gluconeogenic enzymes or both may have low activity in biotin-deficient trout, increased liver glycogen concentrations and altered liver fatty acid compositions may result (Poston and McCartney 1974; Poston 1976a). High concentrations of liver glycogen were reported in biotin-deficient lake trout (Poston 1976a; Poston and Page 1982) and rainbow trout (Castledine et al. 1978). Altered liver fatty acid composition occurred in biotin-deficient brook trout (Poston and McCartney 1974) and rainbow trout (Castledine et al. 1978). Liver lipid concentrations did not vary between channel catfish fed 0% or 8 mg biotin/kg dry diet over a 22-wk period (Robinson and Lovell 1978). Biotin-deficient diets resulted in larger liver size in brook trout compared with individuals fed sufficient dietary biotin (6 mg/kg dry diet) (Poston and McCartney 1974), whereas the presence (8 mg/kg dry diet) or absence of dietary biotin did not affect liver size in channel catfish (Robinson and Lovell 1978).

Inositol

Qualitative requirements for inositol have been reported for rainbow trout (McLaren et al. 1947), brook, brown, and rainbow trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), common carp (Aoe and Masuda 1967), Japanese eel (Arai et al. 1972a), and red sea bream (Yone 1975). General inositol deficiency symptoms include poor feed digestibility and utilization, anorexia, reduced growth, and distended abdomens (Halver 1972a). Skin lesions occurred in common carp fed inositol-deficient diets and included the following physiological and morphological changes: hemorrhage around the base of the dorsal fin, loss of skin mucosa, and "sloughing off" of scales and fins (Aoe and Masuda 1967).

Quantitative inositol requirements are available only for common carp and red sea bream. Common carp require 4 g inositol/kg dry diet for maximal weight gain, feed conversion, and prevention of skin lesions (Aoe and Masuda 1967). Red sea bream require between 550 and 900 mg inositol/kg dry diet in direct proportion to dietary glucose concentrations of 10 to 40% (Yone 1975). Currently, quantitative inositol requirements for salmonids are based upon dietary concentrations (250 to 400 mg/kg dry diet) that were included in the control diets used to determine qualitative vitamin requirements of chinook salmon (Halver 1957).

Vitamin A

Vitamin A has been shown to be an essential dietary constituent for channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967b), common carp (Aoe et al. 1968), goldfish (Jones et al. 1971), and brook trout (Poston et al. 1977). General physiological functions of vitamin A in fish include a role in maintaining normal growth rate, pigmentation, and vision. Long-term feeding studies have consistently yielded various eye malformations (e.g., popeye, cataracts, hermorrhage) in fish fed vitamin A-deficient diets. Rainbow trout fed no supplemental vitamin A in a semipurified diet developed corneal pitting and homogeneous clouding, thickening of the corneal epithelium, and degeneration of the retina (Poston et al. 1977). However, growth during the 22-wk period was similar regardless of dietary vitamin A content (0% vs. 10,000 International Units (IU) vitamin A/kg dry diet). Brook trout of a smaller initial weight (0.15 g) than the rainbow trout fingerlings (5.9 g) grew significantly faster over a 20-wk period when fed 10,000 IU vitamin A/kg dry diet compared with 0% vitamin A (Poston et al. 1977). Pronounced eyeball protrusions and dermal depigmentation occurred in brook trout fed vitamin A-deficient diets. Histopathological examinations of eyes of salmonids have shown that lens damage does not occur in vitamin A-deficient fish (Poston et al. 1977). Vitamin A deficiency symptoms in channel catfish include depigmentation, opaque and protruding eyes, atrophy, and death (Dupree 1970). Vitamin A-deficient goldfish developed exophthalmos, loss of scales, anorexia, and eventual mortality (Jones et al. 1971).

Conversion efficiency of β-carotene to vitamin A has been examined indirectly for channel catfish and brook trout. Dupree (1966) indicated that 12 mg β-carotene/kg dry diet (equal to 20,000 IU of vitamin A/kg dry diet) were insufficient to prevent popeye in channel catfish fed vitamin A-deficient diets, whereas 450 IU of vitamin A/kg dry diet were sufficient to prevent occurrence of popeye in channel catfish fed diets devoid of β-carotene. These results suggested an inefficient conversion rate (if any) of β-carotene to vitamin A in channel catfish (Dupree 1966). In a separate study, channel catfish fingerlings (mean initial weight = 2.25 g) fed 1,000 IU vitamin A acetate had optimal weight gain and no occurrence of popeye or other vitamin A deficiency symptoms (Dupree 1970). Poston et al. (1977) demonstrated indirectly that brook trout can convert dietary β-carotene into vitamin A with conversion efficiency being greater at 12.4°C than at 9°C. Individuals fed 6 mg β-carotene/kg dry diet (10,000 IU vitamin A activity/kg for many terrestrial animals) without supplemental vitamin A did not develop depigmentation or pronounced eyeball protrusion. However, brook trout fed 10,000 IU vitamin A palmitate/kg dry diet without supplemental β-carotene grew significantly better than fish fed 6 mg β-carotene/kg dry diet. Additionally, brook trout fed 0.6 mg β-carotene/kg dry diet (1,000 IU vitamin A activity) during the same experimental period developed pronounced eyeball protrusion at either 9° or 12.4°C.

Vitamin D

Qualitative requirements for cholecalciferol have been determined for channel catfish and rainbow trout. Lovell and Li (1978) demonstrated the essentiality of dietary cholecalciferol for channel catfish fingerlings via greater weight gain and bone mineralization (total body ash, phosphorus, and calcium) in individuals fed 500 IU cholecalciferol/kg dry diet compared with 0% dietary cholecalciferol. Hypervitaminosis was not detected since dietary cholecalciferol concentrations as high as 1,000,000 IU/kg dry diet did not suppress body weight gain nor body fixation of calcium and phosphorus. Barnett et al. (1979a) established the essentiality of cholecalciferol for rainbow trout fingerlings using two dietary concentrations (0% vitamin D_3 compared with 1,000 IU/kg dry diet). These investigators found that symptoms of cholecalciferol deficiency included decreased weight gain and feed efficiency, marked increase in plasma triiodothyronine (T3) levels, lethargy, anorexia, increased lipid content of white muscle and liver, and clinical signs of tetany. Further study of cholecalciferol deficiency in rainbow trout indicated occurrence of tetany of the epaxial musculature (white muscle fibers) and changes in muscle ultrastructure, while red muscle fibers constituting the lateral line musculature appeared to be normal (George et al. 1979). These changes were interpreted as being indicative of disruption of calcium homeostasis. Bone ash, calcium and phosphorus, alkaline phosphatase, plasma calcium, and plasma magnesium were similar in rainbow trout fed either 1,000 IU cholecalciferol/kg dry diet or 0% cholecalciferol. Possibly, feeding dietary cholecalciferol concentrations >1,000 IU/kg to rainbow trout fingerlings would have influenced calcium, phosphorus, or magnesium content of bone or plasma. Plasma T3 concentrations of rainbow trout were unaffected by calcium supplementation of vitamin D-deficient diets and plasma and skeletal calcium levels were unaffected by a limited range of dietary vitamin D content (0 to 1,000 IU cholecalciferol/kg dry diet) (Leatherland et al. 1980).

Relative efficacy of dietary ergocalciferol compared with dietary cholecalciferol was examined in channel catfish fingerlings (Andrews et al. 1980) and rainbow trout fingerlings (Barnett et al. 1979b; Leatherland et al. 1980). Dietary concentrations of 1,000 IU/kg or less promoted similar growth rates when identical amounts of ergocalciferol and cholecalciferol were fed to channel catfish. Comparison of identical dietary concentrations of cholecalciferol and ergocalciferol above 1,000 IU/kg (2,000 to 20,000 IU/kg) resulted in greater weight gain of fingerlings fed cholecalciferol. Based upon weight gain, channel catfish fingerlings (initial mean weight = 2.3 g) require dietary cholecalciferol at greater concentrations than 1,000 IU/kg dry diet, but ≤4,000 IU/kg dry diet (Andrews et al. 1980). Slightly larger channel catfish (initial mean weight = 6.0 g) require dietary cholecalciferol at greater concentrations than 1,000 IU/kg dry diet, but ≤2,000 IU/kg dry diet. Hypervitaminosis occurred in channel catfish fed 50,000 IU/kg of ergocalciferol or cholecalciferol as evidenced by reduced weight gain and feed efficiency. However, vertebral bone ash was not affected by various dietary ergocalciferol or cholecalciferol concentrations. Leatherland et al. (1980) reported that an inverse relationship between T3, a growth stimulating hormone, and dietary vitamin D concentration (cholecalciferol or ergocalciferol) existed in rainbow trout fingerlings. They speculated that hypersecretion of T3 in fish fed vitamin D-deficient diets may be a compensatory response. Cholecalciferol concentrations of 200 or 800 IU/kg promoted slightly better growth of rainbow trout than identical concentrations of ergocalciferol (200 or 800 IU/kg). Also, 800 IU of cholecalciferol/kg was the only dietary vitamin D concentration which significantly reduced T3 concentrations of fish compared with those fed a vitamin D-deficient diet. Barnett et al. (1979b) reported that rainbow trout fingerlings require between 1,600 and 2,400 IU of cholecalciferol/kg dry diet and that cholecalciferol is three times more effective than ergocalciferol in promoting weight gain.

Vitamin E

Vitamin E has been established as an essential dietary component for chinook salmon (Woodall et al. 1964), brown trout (Poston 1965), channel catfish (Dupree 1969b; Murai and Andrews 1974), Atlantic salmon (Poston et al. 1976), common carp (Watanabe et al. 1970a; Watanabe and Takashima 1977), and rainbow trout (Cowey et al. 1981a). Vitamin E deficiency symptoms in channel catfish include poor growth, reduced food conversion, exudative diathesis, muscular dystrophy, depigmentation, fatty livers, anemia, and atrophy of pancreatic tissue (Murai and Andrews 1974). Dietary supplementation of DL-α-tocopherol (25 to 100 mg/kg) fed to channel catfish fingerlings removed all of these deficiency symptoms, whereas an antioxidant, ethoxyquin (125 mg/kg), did not significantly improve hematocrit levels or reduce incidence of muscular dystrophy. Vitamin E deficiency symptoms in chinook salmon included poor growth, exophthalmia, ascites, anemia, clubbed gills, epicarditis, and ceroid deposition in the spleen (Woodall et al. 1964). Brook trout fingerlings fed vitamin E-deficient diets had reduced growth rates, increased mortality, and lower microhematocrit values than did fish fed a diet containing 500 mg of DL-α-tocopherol acetate/kg dry diet (Poston 1965). Atlantic salmon fed vitamin E-deficient diets displayed anemia, pale gills, anisocytosis, poikilocytosis, exudative diathesis, dermal depigmentation, muscular dystrophy, and increased carcass fat and water content (Poston et al. 1976).

Vitamin E has been shown to be important in reproductive physiology of fishes. Adult female common carp (initial mean weight = 100 g) fed a vitamin E-deficient diet for 17 mo displayed reduced weight gain, lower gonadosomatic index, apparent muscular dystrophy (degenerative epaxial muscles), higher muscle water content, lower muscle protein content, and lower concentrations of yolk granules and yolk vesicles in oocytes compared with individuals fed 700 mg α-tocopherol/kg dry diet (Watanabe and Takashima 1977). Also, developing ovaries of common carp fed vitamin E-deficient diets had altered polar lipid fractions in the form of lower concentrations of 20:4ω6, 20:5ω3, and 22:6ω3 and higher concentrations of 18:1ω9 and 20:3ω9.

Quantitative vitamin E requirements of fishes depend upon interaction of several factors: 1) Dietary concentration of polyunsaturated fatty acids, 2) dietary selenium concentration, 3) dietary concentrations of proxidants and antioxidants, 4) diet storage temperature, and 5) length of diet storage. Woodall et al. (1964) reported that a dietary vitamin E concentration of 5 to 30 mg α-tocopherol combined with 5% herring oil provided satisfactory growth of chinook salmon and prevented the occurrence of clinical deficiency symptoms in this species. Common carp fingerlings (initial mean weight = 1.6 g) required about 100 mg α-tocopherol/kg dry diet in order to maintain maximal growth rate and feed efficiency (Watanabe et al. 1970b). Slightly larger common carp fingerlings (initial mean weight = 6.4 g), fed 100 mg or less of DL-α-tocopheryl acetate/kg dry diet concurrently with 5% dietary methyl linoleate as the sole lipid component, displayed apparent muscular dystrophy and had less weight gain than did fish fed 300 mg DL-tocopheryl acetate/kg dry diet plus 5% methyl linoleate (Watanabe et al. 1977). Also, common carp fed 10 or 15% methyl linoleate plus 100 mg DL-α-tocopheryl acetate, had significantly less weight gain and higher occurrence of muscular dystrophy than fish fed 2 or 5% methyl linoleate plus 100 mg DL-α-tocopheryl acetate. Rainbow trout fingerlings (initial mean weight = 0.9 g) fed a diet containing 15% pollock liver oil (in the form of methyl esters) displayed general vitamin E deficiency signs (anorexia and reduced growth), after 6 wk (Watanabe et al. 1981). Diets supplemented with 50 mg α-tocopherol/kg dry diet prevented anorexia and promoted growth rates equal to those fish fed 100, 300, or 500 mg α-tocopherol/kg dry diet. However, the minimal requirement may be slightly <50 mg α-tocopherol/kg dry diet. Larger rainbow trout fingerlings (initial mean weight = 10 g) require 20 to 30 mg DL-α-tocopheryl acetate/kg dry diet when fed 1% 18:3ω3 plus 13% palmitic acid (Cowey et al. 1981a). Dietary vitamin E concentrations <20 mg DL-α-tocopheryl acetate/kg dry diet resulted in higher molar ratios of polyunsaturated fatty acid to tocopherol in rainbow trout livers. Also, in vitro ascorbic acid-stimulated peroxidation in mitochondria and microsomes was significantly higher in rainbow trout fed low dietary vitamin E concentrations (e.g., 0 and 5 mg DL-α-tocopheryl acetate/kg dry diet). Furthermore, these investigators suggested that the vitamin E requirement for rainbow trout is undoubtedly proportionally higher with increasing dietary concentrations of unsaturated fatty acids. Supplementary dietary concentrations of either 33, 66, or 99 IU of DL-α-tocopheryl acetate/kg dry diet added to 20 mg of dietary α-tocopherol/kg dry diet, produced equal growth rates, feed efficiency, and whole body percentage protein, lipid, and moisture of rainbow trout fingerlings fed 12% dietary lipid (Hung et al. 1980). In another study, diets containing 24 mg of α-tocopherol/kg dry diet combined with about 12% dietary lipid, which included 7.5% dietary, unoxidized herring oil, prevented vitamin E deficiency in rainbow trout fingerlings (Hung et al. 1981).

Vitamin K

Dietary supplementation of vitamin K for salmonids has proven beneficial in increasing hematocrit values of brook trout (Poston 1964) and lake trout (Poston 1976b), whereas vitamin K supplementation of diets fed to channel catfish did not enhance blood clotting time or hemoglobin concentrations (Murai and Andrews 1977). Growth of each of the aforementioned species was unaffected by dietary vitamin K supplementation. A dietary concentration of 1 mg menadione dimethylpyrimidinol bisulfite/kg dry diet was sufficient to provide normal coagulation and packed cell volume of lake trout blood (Poston 1976b). Murai and Andrews (1977) concluded that channel catfish have an extremely low, if any, dietary vitamin K requirement, since individuals fed a diet devoid of vitamin K had similar weight gain, blood clotting times, prothrombin times, and hematocrit values to individuals fed up to 1.2 mg menadione sodium bisulfite/kg dry diet.

MINERALS

Calcium and Calcium-to-Phosphorus Ratios

Initial investigations indicated that calcium uptake in fish is primarily through imbibition and gill absorption rather than from dietary sources (Podoliak 1961; Simmons 1971). Nevertheless, since calcium and phosphorus are both major components of fish bone and scales, dietary calcium-to-phosphorus ratios were examined by several investigators to determine if any interactions occur between calcium and phosphorus, which might result in altered bone ash, calcium, and phosphorus content. Dietary calcium did not affect growth and feed efficiency of common carp (Ogino and Takeda 1976), channel catfish (Lovell 1977), and rainbow trout (Ogino and Takeda 1978). However, in a separate study with channel catfish, 1.5% dietary calcium induced maximal weight gain, whereas lower and higher dietary calcium concentrations produced less weight gain (Andrews et al. 1973). Optimal growth and feed conversion occurred in channel catfish fingerlings fed a 1.5:1 ratio of calcium to phosphorus (Andrews et al. 1973) and optimal feed efficiency and serum inorganic phosphorus were observed in red sea bream fed a 1:2 ratio of calcium to phosphorus (Sakamoto and Yone 1973). The difficulty in determining whether dietary calcium-to-phosphorus ratios are nutritionally significant in fish may be complicated by dietary factors such as magnesium and vitamin D or use of suboptimal calcium water concentrations in various studies. Based on the few species studied, it is unknown whether salinity determines if dietary calcium-to-phosphorus ratios are important dietary factors. Optimal dietary calcium-to-phosphorus ratios have been reported for one marine species (red sea bream) and one freshwater species (channel catfish), while no optimal ratios were reported for common carp or rainbow trout.

Phosphorus

Dietary essentiality of phosphorus has been verified for channel catfish (Andrews et al. 1973; Lovell 1978), Atlantic salmon (Ketola 1975a), red sea bream (Yone 1975), common carp (Ogino and Takeda 1976), and rainbow trout (Ogino and Takeda 1978). Deficiency symptoms in channel catfish include reduced growth, poor feed efficiency, low bone ash, and low hematocrit levels (Andrews et al. 1973), and reduced weight gain, bone ash, and bone phosphorus content (Lovell 1978). Red sea bream fed phosphorus-deficient diets contained lower vertebral ash, calcium, and phosphorus and more brittle bone structure (Yone 1975). Common carp and rainbow trout fed diets deficient in phosphorus had reduced calcium, phosphorus, and ash content of whole body and vertebrae (Ogino and Takeda 1976; Ogino and Takeda 1978, respectively). Also, Ogino and Takeda (1976) reported deformity of the frontal bone of the cranium of common carp and spondylolisthesis, brachyospondylie, and synostosis of vertebrae in phosphorus-deficient individuals.

Based on examination of limited sources of phosphorus, dietary phosphorus requirements have been reported as 0.4% or 0.42 to 0.47% for channel catfish (Gatlin et al. 1982; Lovell 1978, respectively), 0.6% inorganic phosphorus supplemented to a diet containing 0.7% phosphorus from plant sources for Atlantic salmon (Ketola 1975a), 0.68% for red sea bream (Yone 1975), 0.6 to 0.7% for common carp (Ogino and Takeda 1976), and 0.7 to 0.8% for rainbow trout (Ogino and Takeda 1978). Supplementation of 0.4 to 2% monosodium, monocalcium, or dicalcium phosphate to diets containing 0.55 to 0.65% available phosphorus did not improve growth or feed efficiency of rainbow trout fingerlings (initial mean weight = 21 g) over an 18-wk period (Reinitz et al. 1978a). Generally, inorganic phosphorus in formulated feeds is more digestible or available for fishes than organic forms of phosphorus occurring in soybean meal and fish meal (Ketola 1975a, b; Lovell 1978).

Magnesium

Magnesium is an essential constituent of bone in fish and is interrelated with calcium metabolism. Whole body and vertebral calcium content were inversely related to dietary magnesium concentration in common carp (Ogino and Chiou 1976) and rainbow trout (Ogino et al. 1978), whereas whole body and vertebral phosphorus content were unaffected by dietary magnesium in the same species. Sakamoto and Yone (1979) concluded that marine fishes have very low (if any) dietary magnesium requirements, since 12 versus 66 mg magnesium/100 g diet fed to red sea bream did not differentially affect growth, vertebral magnesium content, or vertebral calcium content.

Quantitative dietary magnesium requirements for rainbow trout (0.06 to 0.07%) and carp (0.04 to 0.05%) were established based upon one dietary calcium concentration and one calcium and magnesium concentration in ambient water in each study (Ogino et al. 1978; Ogino and Chiou 1976, respectively). Cowey (1976) reported that excessive dietary calcium (2.7%) in relation to dietary magnesium (0.04%) was accompanied by renal nephrocalcinosis in rainbow trout, while 0.1% magnesium fed to rainbow trout along with 2.7% calcium resulted in normal renal calcium concentrations. Further increases in dietary calcium concentrations to 4% required dietary magnesium concentrations of 0.1%, rather than 0.06% magnesium to prevent renal calcinosis (Cowey et al. 1977). Therefore a direct interrelationship was established between dietary calcium and magnesium fed to rainbow trout in freshwater (Cowey 1976).

Manganese

Common carp and rainbow trout fingerlings have been found to have higher growth rates when fed 12 to 13 mg manganese/kg dry diet versus 4 mg manganese/kg dry diet (Ogino and Yang 1980). Manganese-deficient rainbow trout displayed abnormal curvature of the backbone and malformation of the tail.

Zinc

Zinc has been shown to be an essential trace element for rainbow trout in separate studies (Ogino and Yang 1978; Ketola 1979b) and common carp (Ogino and Yang 1979). Dietary zinc concentrations of 15 and 30 mg/kg dry diet fed over an 8-wk period in the presence of 11 μg zinc/l of rearing water promoted satisfactory growth of rainbow trout, while 5 mg zinc/kg dry diet produced slightly slower growth rates (Ogino and Yang 1978). In the same study, rainbow trout fingerlings fed 1 mg zinc/kg dry diet had poor growth, high mortality (46% vs. 0% in other treatments), high incidence of cataracts (49% vs. 0% in other treatments) and high incidence of fin erosion (86% vs. 0% in other treatments). Protein digestibility was appreciably reduced in rainbow trout fed 1 mg zinc/kg dry diet (Ogino and Yang 1978). Although carboxypeptidase activity was not tested, lower activity of this zinc-containing enzyme could explain lower protein digestibility (Ogino and Yang 1978). Ketola (1979b) determined that laboratory diets containing 40% white fish meal (60 mg zinc/kg dry diet) caused bilateral cataracts in rainbow trout, possibly as a result of excesses of other minerals in white fish meal (calcium, phosphorus, sodium, or potassium). Supplementation of 150 mg zinc/kg dry diet to the laboratory diet containing 40% white fish meal and 60 mg zinc/kg dry diet resulted in normal growth rates and prevented cataract formation in rainbow trout. Common carp, fed 1 ppm dietary zinc in the presence of 10 μg zinc/l rearing water over 12- and 16-wk periods in separate studies, had high mortality rates, reduced growth rate, and had fin and skin erosion (Ogino and Yang 1979). No cataract formations were reported in zinc deficient common carp, however. Common carp fingerlings required between 15 and 30 ppm of dietary zinc for optimal growth.

Iron

Dietary iron is essential for fishes to maintain normal hemoglobin content, hematocrit value, and mean corpuscular diameter. Hypochromic, microcytic anemia occurred in red sea bream (Yone 1975) and common carp (Sakamoto and Yone 1978b) as well as anisocytosis in red sea bream fed iron-deficient diets. Control diets fed to red sea bream and common carp, which prevented these iron deficiency symptoms, contained 1.2 g ferric citrate/kg dry diet and 199 mg iron/kg dry diet, respectively. A minimal dietary iron concentration of 150 mg/kg diet is required to prevent iron deficiency symptoms such as low mean corpuscular diameter and low blood iron content in red sea bream (Sakamoto and Yone 1978a).

Copper

Dietary copper requirements have been investigated for channel catfish, common carp, and rainbow trout. Copper requirements, if any, for fingerling channel catfish are ≤1.5 mg/kg dry diet (Murai et al. 1981). Channel catfish fed 9.5 mg copper/kg dry diet while reared in water containing 0.33 μg copper/l for 16 wk grew significantly slower than individuals fed diets containing only 3.5 mg copper/kg dry diet. Further reductions in weight gain occurred in channel catfish fed diets containing 17.5 or 33.5 mg copper/kg dry diet compared with those individuals fed 9.5 mg copper/kg dry diet. Also, a slight reduction occurred in the number of erythrocytes and hematocrit levels in channel catfish fed 33.5 mg copper/kg dry diet resulting in slight anemia. Murai et al. (1981) suggested that since fish can absorb copper from the surrounding water, absorption of environmental copper may result in lower dietary copper requirements than that required by most terrestrial animals. Common carp fingerlings fed 0.7 mg copper/kg dry diet had lower weight gain than individuals fed 3.0 mg copper/kg dry diet (Ogino and Yang 1980). In contrast, no differential growth response occurred in rainbow trout fingerlings fed either 0.7 or 3.0 mg copper/kg dry diet (Ogino and Yang 1980).

Selenium

Selenium is an essential dietary constituent for Atlantic salmon and rainbow trout. Poston et al. (1976) demonstrated dietary essentiality of selenium for Atlantic salmon fry and fingerlings. Deficiency of dietary selenium suppressed glutathione peroxidase activity, while supplements of both vitamin E (500 IU DL-α-tocopheryl acetate/kg) and selenium (0.1 mg/kg dry diet) prevented muscular dystrophy. However, no minimal dietary selenium requirement nor minimal selenium concentration causing toxicity was determined for Atlantic salmon. Dietary selenium concentrations as low as 0.07 mg/kg dry diet prevented selenium deficiency symptoms (i.e., degeneration of liver and muscle) in rainbow trout fingerlings concurrently fed 400 IU vitamin E/kg dry diet while reared in water containing 0.4 μg selenium/l (Hilton et al. 1980). Since selenium is a component of glutathione peroxidase, it is of interest that maximal plasma glutathione peroxidase activity was obtained at a dietary selenium concentration of 0.15 to 0.38 mg/kg dry feed. On the other hand, selenium toxicity occurred in rainbow trout fed dietary selenium concentrations of 13 mg/kg of dry diet, causing reduced growth and feed efficiency and uncoordinated spiral swimming behavior 12 to 24 h before death. Hilton et al. (1980) emphasized the importance of reporting dietary vitamin E concentrations and water borne selenium concentrations when investigating dietary selenium requirements of fish.

Iodine

Iodine has been shown to have a role in thyroid metabolism in fishes similar to that occurring in terrestrial animals. Woodall and LaRoche (1964) examined dietary iodide requirements of chinook salmon fed 0.1 to 10.1 mg iodide/kg diet during an initial 6-mo study and an additional 9-mo study. After 6 mo, no significant differences occurred in growth, feed efficiency, and body composition. However, iodine stored in the thyroid glands of chinook salmon fed 0.1 mg iodide/kg dry diet equaled only 40% of the iodide in individuals fed higher iodide concentrations (0.6, 1.1, 5.1, and 10.1 mg iodide/kg dry diet). The authors concluded that the minimal dietary iodide requirement of chinook salmon fingerlings was about 0.6 mg iodide/kg dry diet based upon the iodide content in thyroid glands. Additionally, they recommended a higher dietary iodide requirement for advanced parr (1.1 mg iodide/kg dry diet) and speculated that smoltification may be accompanied by increased thyroid activity. Increased thyroid activity has been demonstrated in several salmonids during the parr-smolt transformation (Wedemeyer et al. 1980).

SUMMARY AND RECOMMENDATIONS

1) All fish species examined thus far in feeding studies require the same dietary essential amino acids (arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine).
2) Optimal dietary lipid concentrations for maximal protein sparing action in most fish species range from 12 to 24%.
3) Qualitative essential fatty acid requirements and ability to elongate and desaturate fatty acids such as linoleic and linolenic acids are highly variable among fishes, indicating a need for more species-specific research.
4) Relative protein sparing action of carbohydrates and lipids is also highly variable among fish species, necessitating more species-specific research in place of approximating metabolic capabilities of an unstudied species based upon knowledge of other species.
5) Extensive research is needed to determine

nutrient requirements for the striped bass and several coolwater fish species that support important commercial or recreational fisheries, or both.

6) A better understanding of the effects of high dietary fiber on fishes is necessary to evaluate the amount of interference of fiber with enzyme action, changes in transit time of ingested feed in the digestive tract with varying dietary fiber concentrations and effects of dietary fiber on nutrient absorption of fishes.
7) Calcium and magnesium requirements in fishes should be further examined for individual species reared in different calcium and magnesium concentrations or salinities to further determine relative nutritional importance of dietary and water absorption routes of these minerals.
8) Phosphorus requirements of fishes need to be evaluated in conjunction with calcium and magnesium requirements to determine optimal dietary ratios of each macromineral.
9) Knowledge of requirements of fishes for trace elements such as selenium, copper, iron, and zinc is rare, thereby warranting additional research.
10) Better definition of quantitative nutrient requirements of brood stock of various species is necessary to ensure better quality eggs and fry.
11) Regarding better standardization of individual fish nutrition experiments, panelists from a recent fish nutrition workshop have recommended that measurements for metabolizable energy values for experimental diets and digestibility values for macronutrients should be monitored and reported. This is especially important in studies evaluating dietary protein concentration requirements and optimal protein to energy requirements of fishes. Metabolism chambers used by Smith (1971, 1976) are the preferred method.

ACKNOWLEDGMENTS

I am grateful to Gary Rumsey, Hugh Poston, George Ketola, Lowell Sick, Jeanne Joseph, and Paul Bauersfeld for critical review of the manuscript and to Sandra West for typing the manuscript.

LITERATURE CITED

Adron, J. W., A. Blair, C. B. Cowey, and A. M. Shanks.
1976. Effects of dietary energy level and dietary energy source on growth, feed conversion and body composition of turbot (*Scophthalmus maximus* L.). Aquaculture 7: 125-132.

Adron, J. W., D. Knox, C. B. Cowey, and G. T. Ball.
1978. Studies on the nutrition of marine flatfish. The pyridoxine requirement of turbot (*Scophthalmus maximus*). Br. J. Nutr. 40:261-268.

Agrawal, N. K., and C. L. Mahajan.
1980. Hematological changes due to vitamin C deficiency in *Channa punctatus* Bloch. J. Nutr. 110:2172-2181.

Anderson, R. J., E. W. Kienholz, and S. A. Flickinger.
1981. Protein requirements of smallmouth bass and largemouth bass. J. Nutr. 111:1085-1097.

Andrews, J. W.
1977. Protein requirements. *In* R. R. Stickney and R. T. Lovell (editors), Nutrition and feeding of channel catfish, p. 10-13. South. Coop. Ser., Bull. 218.

Andrews, J. W., and T. Murai.
1975. Studies on the vitamin C requirements of channel catfish (*Ictalurus punctatus*). J. Nutr. 105:557-561.
1978. Dietary niacin requirements of channel catfish. J. Nutr. 108:1508-1511.
1979. Pyridoxine requirements of channel catfish. J. Nutr. 109:533-537.

Andrews, J. W., T. Murai, and C. Campbell.
1973. Effects of dietary calcium and phosphorus on growth, food conversion, bone ash and hematocrit levels of catfish. J. Nutr. 103:766-771.

Andrews, J. W., T. Murai, and J. W. Page.
1980. Effects of dietary cholecalciferol and ergocalciferol on catfish. Aquaculture 19:49-54.

Aoe, H., and I. Masuda.
1967. Water-soluble vitamin requirements of carp—II. Requirements for *p*-aminobenzoic acid and inositol. Bull. Jpn. Soc. Sci. Fish. 33:674-680.

Aoe, H., I. Masuda, T. Mimura, T. Saito, and A. Komo.
1968. Requirement of young carp for vitamin A. Bull. Jpn. Soc. Sci. Fish. 34:959-964.

Aoe, H., I. Masuda, T. Mimura, T. Saito, A. Komo, and S. Kitamura.
1969. Water-soluble vitamin requirements of carp—VI. Requirement for thiamine and effects of antithiamines. Bull. Jpn. Soc. Sci. Fish. 35:459-465.

Aoe, H., I. Masuda, T. Saito, and A. Komo.
1967a. Water-soluble vitamin requirements of carp—I. Requirement for vitamin B_2. Bull. Jpn. Soc. Sci. Fish. 33:355-360.

Aoe, H., I. Masuda, T. Saito, and T. Takada.
1967b. Water-soluble vitamin requirements of carp—V. Requirement for folic acid. Bull. Jpn. Soc. Sci. Fish. 33:1068-1071.

Aoe, H., I. Masuda, and T. Takada.
1967c. Water-soluble vitamin requirements of carp—III. Requirements for niacin. Bull. Jpn. Soc. Sci. Fish. 33: 681-685.

Arai, S., T. Nose, and Y. Hashimoto.
1972a. Qualitative requirements of young eels *Anguilla japonica* for water-soluble vitamins and their deficiency symptoms. Bull. (Tokyo) Freshw. Fish. Res. Lab. 22: 69-83.
1972b. Amino acids essential for the growth of eels, *An-*

guilla anguilla and *A. japonica*. Bull. Jpn. Soc. Sci. Fish. 38:753-759.

Ashley, L. M.

1972. Nutritional pathology. *In* J. E. Halver (editor), Fish nutrition, p. 439-537. Acad. Press, N.Y.

Austreng, E., and T. Refstie.

1979. Effect of varying dietary protein level in different families of rainbow trout. Aquaculture 18:145-156.

Barnett, B. J., C. Y. Cho, and S. J. Slinger.

1979a. The essentiality of cholecalciferol in the diets of rainbow trout (*Salmo gairdneri*). Comp. Biochem. Physiol. 63A:291-297.

1979b. The requirement for vitamin D_3, and relative biopotency of dietary vitamins D_2 and D_3 in rainbow trout. (Abstr.) J. Nutr. 109:xxiii.

Bergot, F.

1979a. Carbohydrate in rainbow trout diets: Effects of the level and source of carbohydrate and the number of meals on growth and body composition. Aquaculture 18:157-167.

1979b. Effects of dietary carbohydrates and of their mode of distribution on glycaemia in rainbow trout (*Salmo gairdneri* Richardson). Comp. Biochem. Physiol. 64A: 543-547.

Buhler, D. R., and J. E. Halver.

1961. Nutrition of salmonoid fishes. IX. Carbohydrate requirements of chinook salmon. J. Nutr. 74:307-318.

Castell, J. D.

1979. Review of lipid requirements of finfish. *In* J. E. Halver and K. Tiews (editors), Finfish nutrition and fishfeed technology, Vol. I, p. 59-84. Heenemann, Berl.

Castell, J. D., D. J. Lee, and R. O. Sinnhuber.

1972a. Essential fatty acids in the diet of rainbow trout (*Salmo gairdneri*): lipid metabolism and fatty acid composition. J. Nutr. 102:93-100.

Castell, J. D., R. O. Sinnhuber, D. J. Lee, and J. H. Wales.

1972b. Essential fatty acids in the diet of rainbow trout (*Salmo gairdneri*): physiological symptoms of EFA deficiency. J. Nutr. 102:87-92.

Castell, J. D., R. O. Sinnhuber, J. H. Wales, and D. J. Lee.

1972c. Essential fatty acids in the diet of rainbow trout (*Salmo gairdneri*): growth, feed conversion and some gross deficiency symptoms. J. Nutr. 102:77-86.

Castledine, A. J., and J. T. Buckley.

1980. Distribution and mobility of $\omega 3$ fatty acids in rainbow trout fed varying levels and types of dietary lipids. J. Nutr. 110:675-685.

Castledine, A. J., C. Y. Cho, S. J. Slinger, B. Hicks, and H. S. Bayley.

1978. Influence of dietary biotin level on growth, metabolism and pathology of rainbow trout. J. Nutr. 108:698-711.

Chance, R. E., E. T. Mertz, and J. E. Halver.

1964. Nutrition of salmonoid fishes. XII. Isoleucine, leucine, valine and phenylalanine requirements of chinook salmon and interrelations between isoleucine and leucine for growth. J. Nutr. 83:177-185.

Cho, C. Y., S. J. Slinger, and H. S. Bayley.

1976. Influence of level and type of dietary protein, and of level of feeding on feed utilization by rainbow trout. J. Nutr. 106:1547-1556.

Coates, J. A., and J. E. Halver.

1958. Water-soluble vitamin requirements of silver salmon. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 281, 9 p.

Cowey, C. B.

1976. Use of synthetic diets and biochemical criteria in the assessment of nutrient requirements of fish. J. Fish. Res. Board Can. 33:1040-1045.

1979. Protein and amino acid requirements of finfish. *In* J. E. Halver and K. Tiews (editors), Finfish nutrition and fishfeed technology, Vol. I, p. 3-16. Heenemann, Berl.

Cowey, C. B., and J. R. Sargent.

1972. Fish nutrition. Adv. Mar. Biol. 10:383-492.

1979. Nutrition. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology. Volume VIII: Bioenergetics and growth, p. 1-69. Acad. Press, N.Y.

Cowey, C. B., J. W. Adron, and A. Blair.

1970. Studies on the nutrition of marine flatfish. The essential amino acid requirements of plaice and sole. J. Mar. Biol. Assoc. U.K. 50:87-95.

Cowey, C. B., J. W. Adron, D. Knox, and G. T. Ball.

1975. Studies on the nutrition of marine flatfish. The thiamin requirement of turbot (*Scophthalmus maximus*). Br. J. Nutr. 34:383-390.

Cowey, C. B., J. W. Adron, M. J. Walton, J. Murray, A. Youngsun, and D. Knox.

1981a. Tissue distribution, uptake, and requirement for α-tocopherol of rainbow trout (*Salmo gairdneri*) fed diets with a minimal content of unsaturated fatty acids. J. Nutr. 111:1556-1567.

Cowey, C. B., D. J. Cooke, A. J. Matty, and J. W. Adron.

1981b. Effects of quantity and quality of dietary protein on certain enzyme activities in rainbow trout. J. Nutr. 111:336-345.

Cowey, C. B., D. Knox, J. W. Adron, S. George, and B. Pirie.

1977. The production of renal calcinosis by magnesium deficiency in rainbow trout (*Salmo gairdneri*). Br. J. Nutr. 38:127-135.

Cowey, C. B., J. M. Owen, J. W. Adron, and C. Middleton.

1976. Studies on the nutrition of marine flatfish. The effect of different dietary fatty acids on the growth and fatty acid composition of turbot (*Scophthalmus maximus*). Br. J. Nutr. 36:479-486.

Cowey, C. B., J. A. Pope, J. W. Adron, and A. Blair.

1972. Studies on the nutrition of marine flatfish. The protein requirement of plaice (*Pleuronectes platessa*). Br. J. Nutr. 28:447-456.

Dabrowski, K.

1977. Protein requirements of grass carp fry (*Ctenopharyngodon idella* Val.). Aquaculture 12:63-73.

Davis, A. T., and R. R. Stickney.

1978. Growth responses of *Tilapia aurea* to dietary protein quality and quantity. Trans. Am. Fish. Soc. 107: 479-483.

DeLong, D. C., J. E. Halver, and E. T. Mertz.

1958. Nutrition of salmonoid fishes. VI. Protein requirements of chinook salmon at two water temperatures. J. Nutr. 65:589-599.

Dixon, D. G., and J. W. Hilton.

1981. Influence of available carbohydrate content on tolerance of waterborne copper by rainbow trout, *Salmo gairdneri* Richardson. J. Fish Biol. 19:509-517.

Dupree, H. K.

1966. Vitamins essential for growth of channel catfish, *Ictalurus punctatus*. U.S. Bur. Sport Fish., Wildl. Tech. Pap. 7, 12 p.

1969a. Influence of corn oil and beef tallow on growth of channel catfish. U.S. Bur. Sport Fish., Wildl. Tech. Pap. 27, 13 p.

1969b. Vitamin E requirement of channel catfish. U.S. Bur. Sport Fish., Wildl. Resour. Publ. 77, p. 220-221.

1970. Dietary requirement of vitamin A acetate and beta carotene. U.S. Bur. Sport Fish., Wildl. Resour. Publ. 88, p. 148-150.

Dupree, H. K., E. J. Gauglitz, Jr., A. S. Hall, and C. R. Houle.

1979. Effects of dietary lipids on the growth and acceptability (flavor) of channel catfish (*Ictalurus punctatus*). *In* J. E. Halver and K. Tiews (editors), Finfish nutrition and fishfeed technology, Vol. II, p. 87-103. Heenemann, Berl.

Dupree, H. K., and J. E. Halver.

1970. Amino acids essential for the growth of channel catfish, *Ictalurus punctatus*. Trans. Am. Fish. Soc. 99: 90-92.

Edwards, D. J., E. Austreng, S. Risa, and T. Gjedrem.

1977. Carbohydrate in rainbow trout diets. I. Growth of fish of different families fed diets containing different proportions of carbohydrate. Aquaculture 11:31-38.

Fowler, L. G.

1980. Starting diets for chinook salmon fry. Prog. Fish-Cult. 42:165-166.

1981. Protein and energy relation of starting diets for chinook salmon fry. Prog. Fish-Cult. 43:151-153.

Fujii, M., and Y. Yone.

1976. Studies on nutrition of red sea bream—XIII. Effect of dietary linolenic acid and ω3 polyunsaturated fatty acids on growth and feed efficiency. Bull. Jpn. Soc. Sci. Fish. 42:583-588.

Furuichi, M., and Y. Yone.

1980. Effect of dietary dextrin levels on growth and feed efficiency, and chemical composition of liver and dorsal muscle, and the absorption of dietary protein and dextrin in fishes. Bull. Jpn. Soc. Sci. Fish. 46:225-229.

Garling, D. L., Jr., and R. P. Wilson.

1976. Optimum dietary protein to energy ratio for channel catfish fingerlings, *Ictalurus punctatus*. J. Nutr. 106:1368-1375.

1977. Effects of dietary carbohydrate-to-lipid ratios on growth and body composition of fingerling channel catfish. Prog. Fish-Cult. 39:43-47.

Gatlin, D. M., III, E. H. Robinson, W. E. Poe, and R. P. Wilson.

1982. Phosphorus requirement of channel catfish. (Abstr.) Fed. Proc. 41:787.

George, J. C., B. J. Barnett, C. Y. Cho, and S. J. Slinger.

1979. Impairment of white skeletal muscle in vitamin D_3 deficient rainbow trout. (Abstr.) J. Nutr. 109:xxiii.

Halver, J. E.

1957. Nutrition of salmonoid fishes. III. Water-soluble vitamin requirements of chinook salmon. J. Nutr. 62: 225-243.

1965. Tryptophan requirements of chinook, sockeye and silver salmon. (Abstr.) Fed. Proc. 24, Part 1, 169.

1972a. Fish nutrition. Acad. Press, N.Y., 713 p.

1972b. The role of ascorbic acid in fish disease and tissue repair. Bull. Jpn. Soc. Sci. Fish. 38:79-92.

1979. Vitamin requirements of finfish. *In* J. E. Halver and K. Tiews (editors), Finfish nutrition and fishfeed technology, Vol. I, p. 45-58. Heenemann, Berl.

Halver, J. E., and J. A. Coates.

1957. A vitamin test diet for long-term feeding studies. Prog. Fish-Cult. 19:112-118.

Halver, J. E., and W. E. Shanks.

1960. Nutrition of salmonoid fishes. VIII. Indispensable amino acids for sockeye salmon. J. Nutr. 72:340-346.

Halver, J. E., L. M. Ashley, and R. R. Smith.

1969. Ascorbic acid requirements of coho salmon and rainbow trout. Trans. Am. Fish. Soc. 98:762-771.

Halver, J. E., L. S. Bates, and E. T. Mertz.

1964. Protein requirements for sockeye salmon and rainbow trout. (Abstr.) Fed. Proc. 23, Part 1, 397.

Halver, J. E., D. C. DeLong, and E. T. Mertz.

1957. Nutrition of salmonoid fishes. V. Classification of essential amino acids for chinook salmon. J. Nutr. 63: 95-105.

1959. Methionine and cystine requirements of chinook salmon. (Abstr.) Fed. Proc. 18:527.

Halver, J. E., R. R. Smith, B. M. Tolbert, and E. M. Baker.

1975. Utilization of ascorbic acid in fish. Ann. N.Y. Acad. Sci. 258:81-102.

Hamilton, S. J., P. M. Mehrle, F. L. Mayer, and J. R. Jones.

1981a. Method to evaluate mechanical properties of bone in fish. Trans. Am. Fish. Soc. 110:708-717.

1981b. Mechanical properties of bone in channel catfish as affected by vitamin C and toxaphene. Trans. Am. Fish. Soc. 110:718-724.

Harding, D. E., O. W. Allen, Jr., and R. P. Wilson.

1977. Sulfur amino acid requirement of channel catfish: L-methionine and L-cystine. J. Nutr. 107:2031-2035.

Hardy, R. W., J. E. Halver, and E. L. Brannon.

1979. Effect of dietary protein level on the pyridoxine requirement and disease resistance of chinook salmon. *In* J. E. Halver and K. Tiews (editors), Finfish nutrition and fishfeed technology, Vol. I, p. 253-260. Heenemann, Berl.

Hashimoto, Y., S. Arai, and T. Nose.

1970. Thiamine deficiency symptoms experimentally induced in the eel. Bull. Jpn. Soc. Sci. Fish. 36:791-797.

Hilton, J. W.

1982. The effect of pre-fasting diet and water temperature on liver glycogen and liver weight in rainbow trout, *Salmo gairdneri* Richardson, during fasting. J. Fish. Biol. 20:69-78.

Hilton, J. W., C. Y. Cho, and S. J. Slinger.

1978. Effect of graded levels of supplemental ascorbic acid in practical diets fed to rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 35:431-436.

Hilton, J. W., P. V. Hodson, and S. J. Slinger.

1980. The requirement and toxicity of selenium in rainbow trout (*Salmo gairdneri*). J. Nutr. 110:2527-2535.

Hughes, S. G., R. C. Riis, J. G. Nickum, and G. L. Rumsey.

1981a. Biomicroscopic and histological pathology of the eye in riboflavin deficient rainbow trout (*Salmo gairdneri*). Cornell Vet. 71:269-279.

Hughes, S. G., G. L. Rumsey, and J. G. Nickum.

1981b. Riboflavin requirement of fingerling rainbow trout. Prog. Fish-Cult. 43:167-172.

Hung, S. S. O., C. Y. Cho, and S. J. Slinger.

1980. Measurement of oxidation in fish oil and its effect on vitamin E nutrition of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 37:1248-1253.

1981. Effect of oxidized fish oil, DL-α-tocopheryl acetate and ethoxyquin supplementation on the vitamin E nutrition of rainbow trout (*Salmo gairdneri*) fed practical diets. J. Nutr. 111:648-657.

John, M. J., and C. L. Mahajan.

1979. The physiological response of fishes to a deficiency of cyanocobalamin and folic acid. J. Fish. Biol. 14:127-133.

John, T. M., J. C. George, J. W. Hilton, and S. J. Slinger.
1979. Influence of dietary ascorbic acid on plasma lipid levels in the rainbow trout. Int. J. Vitam. Nutr. Res. 49:400-405.

Jones, J. H., E. B. Bullard, and A. Rodriguez.
1971. The essential nature of vitamin A in the diet of goldfish (*Carassius auratus*). Trans. Am. Fish. Soc. 100:676-681.

Jürss, K.
1978. The effect of pyridoxine deficiency on aminotransferase activity in liver and white muscle of rainbow trout (*Salmo gairdneri* Richardson). Comp. Biochem. Physiol. 61B: 385-389.
1981. The effect of vitamin B_6 deficiency on the free amino acids and two aminotransferases of white muscle from *Salmo gairdneri* Richardson. Comp. Biochem. Physiol. 70B: 829-832.

Kanazawa, A., S. Teshima, and K. Imai.
1980. Biosynthesis of fatty acids in *Tilapia zilli* and the puffer fish. Mem. Fac. Fish., Kagoshima Univ. 29:313-318.

Kanazawa, A., S.-I. Teshima, and K. Ono.
1979. Relationship between essential fatty acid requirements of aquatic animals and capacity for bioconversion of linolenic acid to highly unsaturated fatty acids. Comp. Biochem. Physiol. 63B:295-298.

Kanazawa, A., S. Teshima, M. Sakamoto, and M. A. Awai.
1980a. Requirements of *Tilapia zilli* for essential fatty acids. Bull. Jpn. Soc. Sci. Fish. 46:1353-1356.

Kanazawa, A., S. Teshima, M. Sakamoto, and A. Shinomiya.
1980b. Nutritional requirements of the puffer fish: Purified test diet and the optimum protein level. Bull. Jpn. Soc. Sci. Fish. 46:1357-1361.

Ketola, H. G.
1975a. Requirement of Atlantic salmon for dietary phosphorus. Trans. Am. Fish. Soc. 104:548-551.
1975b. Mineral supplementation of diets containing soybean meal as a source of protein for rainbow trout. Prog. Fish-Cult. 37:73-75.
1976. Choline metabolism and nutritional requirements of lake trout (*Salvelinus namaycush*). J. Anim. Sci. 43: 474-477.
1977. Qualitative requirements and utilization of nutrients: Fishes. *In* M. Rechcigl, Jr. (editor), CRC handbook series in nutrition and food, sect. D, Vol. 1, p. 411-418.
1978. Nutritional requirements and feeding of selected coolwater fishes: A review. Prog. Fish-Cult. 40:127-132.
1979a. Influence of dietary lysine on "fin rot," survival, and growth of fry of rainbow trout. Fish Health News 8(2):vi.
1979b. Influence of dietary zinc on cataracts in rainbow trout (*Salmo gairdneri*). J. Nutr. 109:965-969.
1980. Amino acid requirements of fishes: A review. Proc. 1980 Cornell Nutr. Conf., p. 43-47.

Kissil, G. W., C. B. Cowey, J. W. Adron, and R. H. Richards.
1981. Pyridoxine requirements of the gilthead bream, *Sparus aurata*. Aquaculture 23:243-255.

Kitamura, S., S. Ohara, T. Suwa, and K. Nakagawa.
1965. Studies on vitamin requirements of rainbow trout, *Salmo gairdneri*—I. On the ascorbic acid. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 31:818-826.

Kitamura, S., T. Suwa, S. Ohara, and K. Nakagawa.
1967a. Studies on vitamin requirements of rainbow trout—II. The deficiency symptoms of fourteen kinds of vitamin. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 33:1120-1125.
1967b. Studies on vitamin requirements of rainbow trout—III. Requirement for vitamin A and deficiency symptoms. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 33:1126-1131.

Klein, R. G., and J. E. Halver.
1970. Nutrition of salmonoid fishes: Arginine and histidine requirements of chinook and coho salmon. J. Nutr. 100:1105-1109.

Kloppel, T. M., and G. Post.
1975. Histological alterations on tryptophan-deficient rainbow trout. J. Nutr. 105:861-866.

Leary, D. F., and R. T. Lovell.
1975. Value of fiber in production-type diets for channel catfish. Trans. Am. Fish. Soc. 104:328-332.

Leatherland, J. F., B. J. Barnett, C. Y. Cho, and S. J. Slinger.
1980. Effect of dietary cholecalciferol deficiency on plasma thyroid hormone concentrations in rainbow trout, *Salmo gairdneri* (Pisces, Salmonidae). Environ. Biol. Fish. 5:167-173.

Lee, D. J., and G. B. Putnam.
1973. The response of rainbow trout to varying protein/energy ratios in a test diet. J. Nutr. 103:916-922.

Lee, D. J., J. N. Roehm, T. C. Yu, and R. O. Sinnhuber.
1967. Effect of $\omega 3$ fatty acids on the growth rate of rainbow trout, *Salmo gairdnerii*. J. Nutr. 92:93-98.

Lim, C., and R. T. Lovell.
1978. Pathology of the vitamin C deficiency syndrome in channel catfish (*Ictalurus punctatus*). J. Nutr. 108: 1137-1146.

Lim, C., S. Sukhawongs, and F. P. Pascual.
1979. A preliminary study on the protein requirements of *Chanos chanos* (Forskal) fry in a controlled environment. Aquaculture 17:195-201.

Limsuwan, T., and R. T. Lovell.
1981. Intestinal synthesis and absorption of vitamin B-12 in channel catfish. J. Nutr. 111:2125-2132.

Lovell, R. T.
1972. Protein requirements of cage-cultured channel catfish. Proc. Annu. Conf. Southeast Assoc. Game Fish Comm. 26:357-360.
1973. Essentiality of vitamin C in feeds for intensively fed caged channel catfish. J. Nutr. 103:134-138.
1977. Mineral requirements. *In* R. R. Stickney and R. T. Lovell (editors), Nutrition and feeding of channel catfish, p. 30-32. South. Coop. Ser. Bull. 218.
1978. Dietary phosphorus requirement of channel catfish. Trans. Am. Fish. Soc. 107:617-621.

Lovell, R. T., and Y.-P. Li.
1978. Essentiality of vitamin D in diets of channel catfish (*Ictalurus punctatus*). Trans. Am. Fish. Soc. 107:809-811.

Lovell, R. T., and C. Lim.
1978. Vitamin C in pond diets for channel catfish. Trans. Am. Fish. Soc. 107:321-325.

Mahajan, C. L., and N. K. Agrawal.
1979. Vitamin C deficiency in *Channa punctatus* Bloch. J. Fish. Biol. 15:613-622.
1980a. Nutritional requirement of ascorbic acid by Indian major carp, *Cirrhina mrigala*, during early growth. Aquaculture 19:37-48.
1980b. The role of vitamin C in calcium uptake by fish. Aquaculture 19:287-294.

MAYER, F. L., P. M. MEHRLE, AND P. L. CRUTCHER.
1978. Interaction of toxaphene and vitamin C in channel catfish. Trans. Am. Fish. Soc. 107:326-333.

MAYNARD, L. A., AND J. K. LOOSLI.
1969. Animal nutrition. McGraw-Hill, N.Y., 613 p.

MAZID, M. A., Y. TANAKA, T. KATAYAMA, M. ASADUR RAHMAN, K. L. SIMPSON, AND C. O. CHICHESTER.
1979. Growth response of *Tilapia zilli* fingerlings fed isocaloric diets with variable protein levels. Aquaculture 18:115-122.

MAZID, M. A., Y. TANAKA, T. KATAYAMA, K. L. SIMPSON, AND C. O. CHICHESTER.
1978. Metabolism of amino acids in aquatic animals—III. Indispensable amino acids for *Tilapia zillii*. Bull. Jpn. Soc. Sci. Fish. 44:739-742.

McCARTNEY, T. H.
1971. The comparative utilization of glucose, fructose, and galactose by fingerling brook trout. State N.Y. Conserv. Dep., Fish. Res. Bull. 39:43-52.

McLAREN, B. A., E. KELLER, D. J. O'DONNELL, AND C. A. ELVEHJEM.
1947. The nutrition of rainbow trout. I. Studies of vitamin requirements. Arch. Biochem. Biophys. 15:169-178.

MILLIKIN, M. R.
1982. Effects of dietary protein concentration on growth, feed efficiency, and body composition of age-0 striped bass. Trans. Am. Fish. Soc. 111:373-378.
In press. Separate and interactive effects of dietary protein and lipid concentrations on growth and protein utilization of age-0 striped bass. Trans. Am. Fish. Soc.

MURAI, T., AND J. W. ANDREWS.
1974. Interactions of dietary α-tocopherol, oxidized menhaden oil and ethoxyquin on channel catfish (*Ictalurus punctatus*). J. Nutr. 104:1416-1431.
1975. Pantothenic acid supplementation of diets for catfish fry. Trans. Am. Fish. Soc. 104:313-316.
1977. Vitamin K and anticoagulant relationships in catfish diets. Bull. Jpn. Soc. Sci. Fish. 43:785-794.
1978a. Thiamin requirement of channel catfish fingerlings. J. Nutr. 108:176-180.
1978b. Riboflavin requirement of channel catfish fingerlings. J. Nutr. 108:1512-1517.
1979. Pantothenic acid requirements of channel catfish fingerlings. J. Nutr. 109:1140-1142.

MURAI, T., J. W. ANDREWS, AND J. C. BAUERNFEIND.
1978. Use of L-ascorbic acid, ethocel coated ascorbic acid and ascorbate 2-sulfate in diets for channel catfish, *Ictalurus punctatus*. J. Nutr. 108:1761-1766.

MURAI, T., J. W. ANDREWS, AND R. G. SMITH, JR.
1981. Effects of dietary copper on channel catfish. Aquaculture 22:353-357.

MURRAY, M. W., J. W. ANDREWS, AND H. L. DELOACH.
1977. Effects of dietary protein and environmental temperatures on growth, feed conversion and body composition of channel catfish. J. Nutr. 107:272-280.

NATIONAL RESEARCH COUNCIL.
1973. Nutrient requirements of trout, salmon, and catfish. Nutrient requirements of domestic animals. Nat. Acad. Sci. 11, 57 p.
1977. Nutrient requirements of warmwater fishes. Nutrient requirements of domestic animals. [Rev.] Nat. Acad. Sci. 11, 78 p.
1981. Nutrient requirements of coldwater fishes. Nutrient requirements of domestic animals. Nat. Acad. Sci. 16, 63 p.

NOSE, T.
1979. Summary report on the requirements of essential amino acids for carp. *In* J. E. Halver and K. Tiews (editors), Finfish nutrition and fishfeed technology, Vol. I, p. 145-156. Heenemann, Berl.

NOSE, T., AND S. ARAI.
1972. Optimum level of protein in purified test diet for eel, *Anguilla japonica*. Bull. Freshw. Fish. Res. Lab Tokyo 22:145-155.

NOSE, T., S. ARAI, D.-L. LEE, AND Y. HASHIMOTO.
1974. A note on amino acids essential for growth of young carp. Bull. Jpn. Soc. Sci. Fish. 40:903-908.

OGINO, C.
1965. B vitamins requirements of carp, *Cyprinus carpio*—I. Deficiency symptoms and requirements of vitamin B_6. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 31:546-551.
1967. B vitamins requirements of carp—II. Requirements for riboflavin and pantothenic acid. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 33:351-354.

OGINO, C., AND J. Y. CHIOU.
1976. Mineral requirements in fish—II. Magnesium requirement of carp. Bull. Jpn. Soc. Sci. Fish. 42:71-75.

OGINO, C., AND K. SAITO.
1970. Protein nutrition in fish—I. The utilization of dietary protein by young carp. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 36:250-254.

OGINO, C., AND H. TAKEDA.
1976. Mineral requirements in fish—III. Calcium and phosphorous requirements in carp. Bull. Jpn. Soc. Sci. Fish. 42:793-799.
1978. Requirement of rainbow trout for dietary calcium and phosphorus. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 44:1019-1022.

OGINO, C., AND G.-Y. YANG.
1978. Requirements of rainbow trout for dietary zinc. Bull. Jpn. Soc. Sci. Fish. 44:1015-1018.
1979. Requirement of carp for dietary zinc. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 45:967-969.
1980. Requirements of carp and rainbow trout for dietary manganese and copper. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 46:455-458.

OGINO, C., F. TAKASHIMA, AND J. Y. CHIOU.
1978. Requirement of rainbow trout for dietary magnesium. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 44:1105-1108.

OGINO, C., N. UKI, T. WATANABE, Z. IIDA, AND K. ANDO.
1970a. B vitamin requirements of carp—IV. Requirement for choline. Bull. Jpn. Soc. Sci. Fish. 36:1140-1146.

OGINO, C., T. WATANABE, J. KAKINO, N. IWANAGA, AND M. MIZUNO.
1970b. B vitamin requirements of carp—III. Requirement for biotin. Bull. Jpn. Soc. Sci. Fish. 36:734-740.

ORME, L. E.
1978. The status of coolwater fish diets. *In* R. L. Kendell (editor), Selected coolwater fishes of North America, p. 167-171. Am. Fish. Soc. Spec. Publ. 11.

OWEN, J. M., J. W. ADRON, J. R. SARGENT, AND C. B. COWEY.
1972. Studies on the nutrition of marine flatfish. The effect of dietary fatty acids on the tissue fatty-acids of the plaice *Pleuronectes platessa*. Mar. Biol. (Berl.) 13:160-166.

PAGE, J. W.
1978. Dietary sulfur requirements of fish; nutritional,

pathological and biochemical criteria. Ph.D. Thesis, Cornell Univ., 175 p.

Page, J. W., and J. W. Andrews.
1973. Interactions of dietary levels of protein and energy on channel catfish (*Ictalurus punctatus*). J. Nutr. 103:1339-1346.

Page, J. W., G. L. Rumsey, R. C. Riis, and M. L. Scott.
1978. Dietary sulfur requirements of fish: Nutritional and pathological criteria. (Abstr.) Fed. Proc. 37:435.

Phillips, A. M., Jr.
1959a. Vitamin requirement of Atlantic salmon. State N.Y. Conserv. Dep., Fish. Res. Bull. 22:79-81.
1959b. Vitamin requirement of lake trout. State N.Y. Conserv. Dep., Fish. Res. Bull. 22:82-84.
1963. Folic acid as an anti-anemia factor for brook trout. Prog. Fish-Cult. 25:132-134.

Phillips, A. M., Jr., and D. R. Brockway.
1957. The nutrition of trout. IV. Vitamin requirements. Prog. Fish-Cult. 19:119-123.

Podoliak, H. A.
1961. Relation between water temperature and metabolism of dietary phosphorus by fingerling brook trout. Trans. Am. Fish. Soc. 90:398-403.

Poston, H. A.
1964. Effect of dietary vitamin K and sulfaguanidine on blood coagulation time, microhematocrit, and growth of immature brook trout. Prog. Fish-Cult. 26:59-64.
1965. Effect of dietary vitamin E on microhematocrit, mortality and growth of immature brown trout. State N.Y. Conserv. Dep., Fish. Res. Bull. 28:6-9.
1967. Effect of dietary L-ascorbic acid on immature brook trout. State N.Y. Conserv. Dep., Fish. Res. Bull. 30:46-51.
1976a. Optimum level of dietary biotin for growth, feed utilization, and swimming stamina of fingerling lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 33:1803-1806.
1976b. Relative effect of two dietary water-soluble analogues of menaquinone on coagulation and packed cell volume of blood of lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 33:1791-1793.
1978. Neuroendocrine mediation of photoperiod and other environmental influences on physiological responses in salmonids: A review. U.S. Fish Wildl. Serv., Tech. Pap. 96, 14 p.

Poston, H. A., and G. F. Combs, Jr.
1980. Nutritional implications of tryptophan catabolizing enzymes in several species of trout and salmon. Proc. Soc. Exp. Biol. Med. 163:452-454.

Poston, H. A., and R. N. DiLorenzo.
1973. Tryptophan conversion to niacin in the brook trout (*Salvelinus fontinalis*). Proc. Soc. Exp. Biol. Med. 144: 110-112.

Poston, H. A., and T. H. McCartney.
1974. Effect of dietary biotin and lipid on growth, stamina, lipid metabolism and biotin-containing enzymes in brook trout (*Salvelinus fontinalis*). J. Nutr. 104:315-322.

Poston, H. A., and J. W. Page.
1982. Gross and histological signs of dietary deficiencies of biotin and pantothenic acid in lake trout, *Salvelinus namaycush*. Cornell Vet. 72:242-261.

Poston, H. A., G. F. Combs, Jr., and L. Leibovitz.
1976. Vitamin E and selenium interrelations in the diet of Atlantic salmon (*Salmo salar*): gross, histological and biochemical deficiency signs. J. Nutr. 106:892-904.

Poston, H. A., R. C. Riis, G. L. Rumsey, and H. G. Ketola.
1977. The effect of supplemental dietary amino acids, minerals and vitamins on salmonids fed cataractogenic diets. Cornell Vet. 67:472-509.

Prejs, A., and M. Blaszczyk.
1977. Relationships between food and cellulase activity in freshwater fishes. J. Fish. Biol. 11:447-452.

Refstie, T., and E. Austreng.
1981. Carbohydrate in rainbow trout diets. III. Growth and chemical composition of fish from different families fed four levels of carbohydrate in the diet. Aquaculture 25:35-49.

Reinitz, G. L., and F. Hitzel.
1980. Formulation of practical diets for rainbow trout based on desired performance and body composition. Aquaculture 19:243-252.

Reinitz, G. L., L. E. Orme, and F. N. Hitzel.
1978a. Phosphorus requirement for rainbow trout. Feedstuffs 50:17.

Reinitz, G. L., L. E. Orme, C. A. Lemm, and F. N. Hitzel.
1978b. Influence of varying lipid concentrations with two protein concentrations in diets for rainbow trout (*Salmo gairdneri*). Trans. Am. Fish. Soc. 107:751-754.

Ringrose, R. C.
1971. Calorie-to-protein ratio for brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 28:1113-1117.

Robinson, E. H., O. W. Allen, Jr., W. E. Poe, and R. P. Wilson.
1978. Utilization of dietary sulfur compounds by fingerling channel catfish: L-methionine, DL-methionine, methioning hydroxy analogue, taurine and inorganic sulfate. J. Nutr. 108:1932-1936.

Robinson, E. H., and R. T. Lovell.
1978. Essentiality of biotin for channel catfish *Ictalurus punctatus* fed lipid and lipid-free diets. J. Nutr. 108: 1600-1605.

Robinson, E. H., W. E. Poe, and R. P. Wilson.
1980. Quantitative amino acid requirements for channel catfish. Feedstuffs 52(43):29, 36.
1982. Effects of feeding diets containing an imbalance of branched chain amino acids on fingerling channel catfish. (Abstr.) Fed. Proc. 41:540.

Robinson, E. H., R. P. Wilson, and W. E. Poe.
1980a. Total aromatic amino acid requirement, phenylalanine requirement and tyrosine replacement value for fingerling channel catfish. J. Nutr. 110:1805-1812.
1980b. Re-evaluation of the lysine requirement and lysine utilization by fingerling channel catfish. J. Nutr. 110: 2313-2316.
1981. Arginine requirement and apparent absence of a lysine-arginine antagonist in fingerling channel catfish. J. Nutr. 111:46-52.

Rumsey, G. L.
1978. Recent advances in nutrition of salmonids. Salmonid 2(4):14-17, 21, 26.

Rumsey, G. L., and H. G. Ketola.
1975. Amino acid supplementation of casein in diets of Atlantic salmon (*Salmo salar*) fry and of soybean meal for rainbow trout (*Salmo gairdneri*) fingerlings. J. Fish. Res. Board Can. 32:422-426.

Sabaut, J. J., and P. Luquet.
1973. Nutritional requirements of the gilthead bream *Chrysophrys aurata*. Quantitative protein requirements. Mar. Biol. (Berl.) 18:50-54.

Sakaguchi, H., F. Takeda, and K. Tange.
1969. Studies on vitamin requirements by yellowtail—I.

Vitamin B_6 and vitamin C deficiency symptoms. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 35:1201-1206.

Sakamoto, S., and Y. Yone.

1973. Effect of dietary calcium/phosphorus ratio upon growth, feed efficiency and blood serum Ca and P level in red sea bream. Bull. Jpn. Soc. Sci. Fish. 39:343-348.

1978a. Requirement of red sea bream for dietary iron—II. Bull. Jpn. Soc. Sci. Fish. 44:223-225.

1978b. Iron deficiency symptoms of carp. Bull. Jpn. Soc. Sci. Fish. 44:1157-1160.

1979. Requirement of red sea bream for dietary Mg. Bull. Jpn. Soc. Sci. Fish. 45:57-60.

Sandholm, M., R. R. Smith, J. C. H. Shih, and M. L. Scott.

1976. Determination of antitrypsin activity on agar plates: Relationship between antitrypsin and biological value of soybean for trout. J. Nutr. 106:761-766.

Satia, B. P.

1974. Quantitative protein requirements of rainbow trout. Prog. Fish-Cult. 36:80-85.

Sato, M., R. Yoshinaka, and S. Ikeda.

1978. Dietary ascorbic acid requirement of rainbow trout for growth and collagen formation. Bull. Jpn. Soc. Sci. Fish. 44:1029-1035.

Shanks, W. E., G. D. Gahimer, and J. E. Halver.

1962. The indispensable amino acids for rainbow trout. Prog. Fish-Cult. 24:68-73.

Simmons, D. J.

1971. Calcium and skeletal tissue physiology in teleost fishes. Clin. Orthop. Relat. Res. 76:244-280.

Sinnhuber, R. O., D. J. Lee, J. H. Wales, and J. L. Ayres.

1968. Dietary factors and hepatoma in rainbow trout (*Salmo gairdneri*). II. Cocarcinogenesis by cyclopropenoid fatty acids and the effect of gossypol and altered lipids on aflatoxin-induced liver cancer. J. Natl. Cancer Inst. 41:1293-1301.

Sinnhuber, R. O., J. H. Wales, J. D. Hendricks, G. B. Putnam, J. E. Nixon, and N. E. Pawlowski.

1977. Trout bioassay of mycotoxins. *In* J. V. Rodricks, C. W. Hesseltine and M. A. Mehlman (editors), Mycotoxins in human and animal health, p. 731-744. Pathotox Publ., Park Forest South, Ill.

Smith, C. E., M. Brin, and J. E. Halver.

1974. Biochemical, physiological and pathological changes in pyridoxine-deficient rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 31:1893-1898.

Smith, C. E., and J. E. Halver.

1969. Folic acid anemia in coho salmon. J. Fish. Res. Board Can. 26:111-114.

Smith, C. E., M. D. Osborne, R. G. Piper, and W. P. Dwyer.

1979. Effect of diet composition on performance of rainbow trout brood stock during a three-year period. Prog. Fish-Cult. 41:185-188.

Smith, R. R.

1971. A method for measuring digestibility and metabolizable energy of feeds. Prog. Fish-Cult. 33:132-134.

1976. Metabolizable energy of feedstuffs for trout. Feedstuffs 48(23):16, 21.

Smith, R. R., M. C. Peterson, and A. C. Allred.

1980. Effect of leaching on apparent digestion coefficients of feedstuffs for salmonids. Prog. Fish-Cult. 42:195-199.

Smith, R. R., G. L. Rumsey, and M. L. Scott.

1978. Heat increment associated with dietary protein, fat, carbohydrate and complete diets in salmonids: Comparative energetic efficiency. J. Nutr. 108:1025-1032.

Stickney, R. R.

1977. Lipids in catfish nutrition. *In* R. R. Stickney and R. T. Lovell (editors), Nutrition and feeding of channel catfish, p. 14-18. South. Coop. Ser. Bull. 218.

Stickney, R. R., and J. W. Andrews.

1971. Combined effects of dietary lipids and environmental temperature on growth, metabolism and body composition of channel catfish (*Ictalurus punctatus*). J. Nutr. 101:1703-1710.

1972. Effects of dietary lipids on growth, food conversion, lipid and fatty acid composition of channel catfish. J. Nutr. 102:249-258.

Takeuchi, L., T. Takeuchi, and C. Ogino.

1980. Riboflavin requirements in carp and rainbow trout. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 46:733-737.

Takeuchi, T., S. Arai, T. Watanabe, and Y. Shimma.

1980. Requirement of eel *Anguilla japonica* for essential fatty acids. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 46:345-353.

Takeuchi, T., and T. Watanabe.

1977. Effect of eicosapentaenoic acid and docosahexaenoic acid in pollock liver oil on growth and fatty acid composition of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 43:947-953.

Takeuchi, T., T. Watanabe, and T. Nose.

1979. Requirement for essential fatty acids of chum salmon (*Oncorhynchus keta*) in freshwater environment. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 45:1319-1323.

Thompson, B. G.

1981. Fisheries of the United States, 1980. U.S. Dep. Commer., NOAA, NMFS Cur. Fish. Stat. 8100, 132 p.

Tomiyama, T., and N. Ohba.

1967. Biotin requirement of goldfish. [In Jpn., Engl. Abstr.] Bull. Jpn. Soc. Sci. Fish. 33:448-452.

Watanabe, T., and F. Takashima.

1977. Effect of α-tocopherol deficiency on carp—VI. Deficiency symptoms and changes of fatty acid and triglyceride distributions in adult carp. Bull. Jpn. Soc. Sci. Fish. 43:819-830.

Watanabe, T., F. Takashima, and C. Ogino.

1974. Effect of dietary methyl linolenate on growth of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 40:181-188.

Watanabe, T., F. Takashima, C. Ogino, and T. Hibiya.

1970a. Effects of α-tocopherol deficiency on carp. Bull. Jpn. Soc. Sci. Fish. 36:623-630.

1970b. Requirement of young carp for α-tocopherol. Bull. Jpn. Soc. Sci. Fish. 36:972-976.

Watanabe, T., T. Takeuchi, M. Matsui, C. Ogino, and T. Kawabata.

1977. Effect of α-tocopherol deficiency on carp—VII. The relationship between dietary levels of linoleate and α-tocopherol requirement. Bull. Jpn. Soc. Sci. Fish. 43:935-946.

Watanabe, T., T. Takeuchi, and C. Ogino.

1975. Effect of dietary methyl linoleate and linolenate on growth of carp—II. Bull. Jpn. Soc. Sci. Fish. 41:263-269.

Watanabe, T., T. Takeuchi, M. Wada, and R. Uehara.

1981. The relationship between dietary lipid levels and α-tocopherol requirement of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 47:1463-1471.

Watanabe, T., O. Utsue, I. Kobayashi, and C. Ogino.

1975. Effect of dietary methyl linoleate and linolenate on growth of carp—I. Bull. Jpn. Soc. Sci. Fish. 41:257-262.

Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke.

1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42(6):1-14.

Wilson, R. P., O. W. Allen, Jr., E. H. Robinson, and W. E. Poe.

1978. Tryptophan and threonine requirements of fingerling channel catfish. J. Nutr. 108:1595-1599.

Wilson, R. P., D. E. Harding, and D. L. Garling, Jr.

1977. Effect of dietary pH on amino acid utilization and lysine requirement of fingerling channel catfish. J. Nutr. 107:166-170.

Wilson, R. P., and W. E. Poe.

1973. Impaired collagen formation in the scorbutic channel catfish. J. Nutr. 103:1359-1364.

Wilson, R. P., E. H. Robinson, and W. E. Poe.

1981. Apparent and true availability of amino acids from common feed ingredients for channel catfish. J. Nutr. 111:923-929.

Winfree, R. A., and R. R. Stickney.

1981. Effects of dietary protein and energy on growth, feed conversion efficiency and body composition of *Tilapia aurea*. J. Nutr. 111:1001-1012.

Woodall, A. N., L. M. Ashley, J. E. Halver, H. S. Olcott, and J. van der Veen.

1964. Nutrition of salmonoid fishes. XIII. The α-tocopherol requirement of chinook salmon. J. Nutr. 84:125-135.

Woodall, A. N., and G. LaRoche.

1964. Nutrition of salmonoid fishes. XI. Iodide requirements of chinook salmon. J. Nutr. 82:475-482.

Woodward, B.

1982. Riboflavin supplementation of diets for rainbow trout. J. Nutr. 112:908-913.

Yamada, K., K. Kobayashi, and Y. Yone.

1980. Conversion of linolenic acid to $\omega 3$-highly unsaturated fatty acids in marine fishes and rainbow trout. Bull. Jpn. Soc. Sci. Fish. 46:1231-1233.

Yingst, W. L., III, and R. R. Stickney.

1979. Effects of dietary lipids on fatty acid composition of channel catfish fry. Trans. Am. Fish. Soc. 108:620-625.

1980. Growth of caged channel catfish fingerlings reared on diets containing various lipids. Prog. Fish-Cult. 42:24-26.

Yone, Y.

1975. Nutritional studies of red sea bream. Proc. First Int. Conf. Aquaculture Nutr., p. 39-64.

Yoshinaka, R., M. Sato, and S. Ikeda.

1978. *In vitro* formation of collagen in skin of ascorbic acid-deficient rainbow trout. Bull. Jpn. Soc. Sci. Fish. 44:1147-1150.

Yu, T. C., and R. O. Sinnhuber.

1972. Effect of dietary linolenic acid and docosahexaenoic acid on growth and fatty acid composition of rainbow trout (*Salmo gairdneri*). Lipids 7:450-454.

1975. Effect of dietary linolenic and linoleic acids on growth and lipid metabolism of rainbow trout (*Salmo gairdneri*). Lipids 10:63-66.

1976. Growth response of rainbow trout (*Salmo gairdneri*) to dietary $\omega 3$ and $\omega 6$ fatty acids. Aquaculture 8:309-317.

1979. Effect of dietary $\omega 3$ and $\omega 6$ fatty acids on growth and feed conversion efficiency of coho salmon (*Oncorhynchus kisutch*). Aquaculture 16:31-38.

Yu, T. C., R. O. Sinnhuber, and J. D. Hendricks.

1979. Reproduction and survival of rainbow trout (*Salmo gairdneri*) fed linolenic acid as the only source of essential fatty acids. Lipids 14:572-575.

Yu, T. C., R. O. Sinnhuber, and G. B. Putnam.

1977. Use of swine fat as an energy source in trout rations. Prog. Fish-Cult. 39:95-97.

Zeitoun, I. H., J. E. Halver, D. E. Ullrey, and P. I. Tack.

1973. Influence of salinity on protein requirements of rainbow trout (*Salmo gairdneri*) fingerlings. J. Fish. Res. Board Can. 30:1867-1873.

Zeitoun, I. H., D. E. Ullrey, J. E. Halver, P. I. Tack, and W. T. Magee.

1974. Influence of salinity on protein requirements of coho salmon (*Oncorhynchus kisutch*) smolts. J. Fish. Res. Board Can. 31:1145-1148.

ANALYSIS OF DOUBLE-TAGGING EXPERIMENTS

JERRY A. WETHERALL[1]

ABSTRACT

Statistics arising from double-tagging experiments may be applied to estimate tag-shedding probabilities directly, to estimate parameters of underlying theoretical shedding models, or to estimate mortality rates free of tag-shedding bias.

Simple maximum likelihood estimators of tag retention rates, along with their asymptotic variances, may be derived assuming conditional multinomial sampling models. If specific models of shedding are of interest, limitations of existing theory may be reduced by assuming the Type II shedding rate is time-dependent. In the more realistic models and their simpler precursors, parameters may be estimated by least squares or by maximum likelihood methods. Complications arising in the direct maximization of the conditional likelihood may be circumvented by use of iteratively reweighted Gauss-Newton algorithms available in standard statistical software packages. Simple diagnostic plots may be helpful in model selection.

When a sequence of double-tagged cohorts is released, recapture statistics may be treated separately or combined to estimate common shedding rates, but a more general linear model may be used to fully exploit the structure of the experiment and to estimate both common parameters and those unique to each cohort.

When recapture times are unknown but the experiment spans a sufficiently long period, the ratio of constant Type II tag-shedding rate to constant Type II total mortality rate may be estimated. Under similar circumstances, but with exact recapture times known for each fish, maximum likelihood estimates of both parameters may be computed.

If only the Type II mortality rate is of interest, it may be estimated free of tag-shedding bias by simple linear regression of appropriate double-tagging statistics, if Type II shedding and Type II mortality are constant during the experiment.

The estimation of fishing mortality rate, exploitation rate, and population size through mark and recapture experiments is often complicated by the incidental shedding or loss of marks. Failure to account for tag shedding may lead to biased parameter estimates. Thus a well-designed tagging experiment will incorporate some provision for estimating shedding rates and computing correction factors.

The approach usually taken is to release a group, or perhaps several groups of double-tagged fish, and then to estimate shedding rates using information on the number of fish returned in a sequence of recapture samples still bearing both tags and on the number of returns with only one tag remaining. A variety of statistical methods and estimation procedures have been developed. Papers by Beverton and Holt (1957), Gulland (1963), Chapman et al. (1965), Robson and Regier (1966), Chapman (1969), Bayliff and Mobrand (1972), Seber (1973), Laurs et al. (1976), Arnason and Mills (1981), Kirkwood (1981), and Seber and Felton (1981) are particularly noteworthy. In recent years attention has focused primarily on the regression methods developed by Chapman et al. (1965) and extended first by Bayliff and Mobrand (1972) and most recently by Kirkwood (1981).

Despite the extensive literature on double-tagging there is need for an integration of existing thought and for development of new ideas and statistical methods. Accordingly, this paper surveys basic tag-shedding theory and the most widely used analytical techniques, and describes a variety of new models and estimation procedures. Left unaddressed are several important aspects of planning double-tagging experiments. These are the subject of a companion paper by Wetherall and Yong (1981).

TAG LOSS IN SINGLE-TAGGING EXPERIMENTS

To establish a context for later derivations we begin by reviewing the process of tag loss in a population of single-tagged fish. In such a popu-

---

[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

Manuscript accepted April 1982.

lation, losses may be caused by fishing mortality or recapture, natural mortality, tagging mortality (mortality induced by the application or presence of the tag), permanent emigration, or by tag shedding. In addition, recaptured tags are considered "lost" if not detected in the catch and recovered, or, when recovered, if not returned or reported.

Beverton and Holt (1957) recognized two kinds of losses, which they designated Type I and Type II (these are called Type A and Type B by Ricker 1975). Type I losses are those which, in effect, reduce the number of tags initially put out. They result from the pulse of tagging mortality and tag shedding occurring immediately after release (or in a relatively brief period following release) and from the nonrecovery and nonreporting of tag recaptures. Type II losses are those happening steadily and gradually over an extended period following release of the tagged fish.

These relations may be stated more succinctly in a simple mathematical model. Let $E(r_i)$ denote the expected number of returns of tags recaptured in the ith time interval following the release of $N_s(0)$ single-tagged fish. Then

$$E(r_i) = \pi\,\rho\,N_s(0)\int_{t_i}^{t_i+\Delta_i} F(u)\,\zeta(u)\,\exp\left(-\int_0^u H(x)\,dx\right)du$$

where t_i = time at the beginning of interval i

Δ_i = length of time interval i

$1-\pi$ = probability that a tag is lost due to immediate tagging mortality

$1-\rho$ = probability that a tag is shed immediately following release

$F(u)$ = instantaneous fishing mortality rate at time u

$1-\zeta(u)$ = probability that a tag recaptured at time u is not recovered and reported (a Type I loss)

$H(x)$ = total instantaneous rate of Type II tag loss at time x.

Here $H(x)$ represents the unspecified combined effects of fishing mortality, $F(x)$, natural mortality, $M(x)$, instantaneous tag shedding, $L(x)$, and remaining losses, $G(x)$. The usual assumptions are that the Type II losses operate in the manner of independent Poisson processes with constant rates and that the recovery and reporting rates also are constant. Under these conditions the model takes the familiar form

$$E(r_i) = \eta\,N_s(0)\left(\frac{F}{F+X}\right)\left(1-\exp(-(F+X)\Delta_i)\right)\left(\exp(-(F+X)t_i)\right) \qquad (1)$$

where $\eta = \pi\,\rho\,\zeta$
$X = M + L + G.$

A variety of estimation schemes based on this equation have been developed, notably by Paulik (1963). These have been reviewed along with other mark-and-recapture approaches by Cormack (1968) and Seber (1973). The importance of assumptions on Type I and Type II losses in these procedures depends on which parameters are of central concern in the experiment. In fisheries applications the parameter most often focused on is the fishing mortality rate, F. Paulik's single-release regression model with constant Δ, for estimating F and the exploitation rate, $\mu = (F/(F+M))[1-\exp(-(F+M)\Delta)]$ stems directly from Equation (1). In this situation, if Type I losses are present the model will estimate ηF rather than F. Subsequent estimates of X will be too large. Further, estimates of the exploitation rate will be negatively biased, and if these are used along with $N_s(0)$ to estimate total population sizes, such estimates will be inflated. Of course, this is the general effect of Type I losses on Petersen estimates.

If Type II tagging mortality or Type II tag shedding occur, the estimate of F from this single-release model will not be affected, but the estimate of μ will be less than the true exploitation rate of the unmarked population.

Sometimes all recaptures are made during subintervals of equal length imbedded and irregularly spaced within the total recapture period (e.g., in a salmon fishery with a complex pattern of open and closed periods). In this case, Paulik shows that the single-release model based on Equation (1) will give estimates of F and X

which are unaffected by Type I losses, and in fact will yield an estimate of η as well as the usual estimates of F and X. Since the conditions required for this scheme will not often be encountered, it will usually be necessary to conduct a multiple-release experiment, with at least one preseason release, in order to obtain separate estimates of F, X, and η. Models appropriate to this situation have also been extensively developed by Paulik (1963).

However, even in the multiple-release models the Type II tagging mortality and Type II shedding will generate an underestimate of the true exploitation rate. Thus while the problems imposed by Type I losses may be circumvented by more elaborate experimental designs, the undesired effects of Type II losses remain. Two remedies are possible: 1) The single-tagging may be supplemented with a double-tagging experiment and other special studies to estimate Type II components and determine correction factors, or 2) double-tagging may be used exclusively to estimate mortality rates unaffected by Type I and Type II shedding. Both strategies are treated below. We note here that even when tag shedding and mortality are not the chief concerns of a tagging experiment, double-tagging is often employed simply to increase expected recovery rates (e.g., Hynd 1969; Bayliff 1973).

MODELS OF DOUBLE-TAGGING

We restrict our attention to the case where members of the population are marked with two tags differing in position of attachment and possibly type (call these Type A and Type B). We assume the burden of carrying both tags is equal to the stress of carrying either one alone. Further, we assume that the probabilities of loss are the same for each tag of a specified type and independent of the status of the other tag. Suppose a cohort of fish is double-tagged at time 0. For any fish still alive at time t, the probability that the Type A tag has been shed can be stated as

$$\Omega_A(t) = 1 - \rho_A g_A(t)$$

where $g_A(t) = \exp\left(- \int_0^t L_A(u)\ du\right)$.

An analogous expression exists with respect to tag B. Where shedding rates are assumed to be the same for tag Types A and B the subscripts can be dropped, i.e., the common probability of shedding by time t is

$$\Omega(t) = 1 - \rho g(t). \qquad (2)$$

If we set $L(u) = L(\text{constant})$, Equation (2) embodies the assumptions of Bayliff and Mobrand (1972)—Type II shedding is a simple Poisson process with an identical constant rate for each tag, so that each tag has the same probability of shedding by time t. Moreover, in due course all surviving fish will have shed both tags as long as $L > 0$, i.e., $\Omega(\infty) \to 1$.

The validity of this particular set of assumptions has recently been challenged by results of tag-shedding studies with northwest Atlantic bluefin tuna, *Thunnus thynnus*, (Baglin et al. 1980) and with southern bluefin tuna, *T. maccoyii*, (Kirkwood 1981). In the former case, it was found that the Type II shedding rate increased with time. In Kirkwood's analysis it was apparent that the Type II rate decreased markedly over time. Therefore, it clearly would be advantageous to construct a model permitting time-dependent Type II shedding rates. Kirkwood approached this problem by attacking the common assumption of uniform shedding probabilities among all fish in the cohort. Instead, he considered the Type II shedding rate for each tag applied to be constant over time, but further assumed that the rate for each tag was a random variable with specified probability density. In this light, the deterministic model at Equation (2) is replaced by the expectation $J(t) = E[\Omega(t)] = 1 - \rho\ E[g(t)]$. The average time-varying shedding rate at time t may now be defined as

$$\Psi(t) = \frac{E\{g(t) \cdot L\}}{E\{g(t)\}}$$

where the expectations are taken with respect to the probability density of L. Following standard principles of reliability theory, this may be reduced to

$$\Psi(t) = - \frac{\partial \ln E\{g(t)\}}{\partial t}.$$

Under Kirkwood's assumptions $\Psi(t)$ will decrease with time as long as there is variation in shedding rate among tags, i.e., there will be a continuous culling of tags with relatively high shedding probabilities. This concept is clearly an attractive alternative to the Bayliff-Mobrand model.

Problems in which the instantaneous loss rate is treated as a random variable arise in a variety of contexts ranging from bioassay to analysis of labor turnover in corporations. Because of its unimodality and mathematical tractability, the distribution often selected to describe this variation is the gamma distribution with mean λ and variance λ^2/b (e.g., see Bartholomew 1973:186 or McNolty et al. 1980). As Kirkwood (1981) showed, for the tag-shedding problem, this choice leads to

$$J(t) = 1 - \rho\left(\frac{b}{b + \lambda t}\right)^{\mathrm{b}} \qquad (3)$$

so that

$$\Psi(t) = \frac{b\lambda}{b + \lambda t}\ .$$

The Bayliff-Mobrand model is now seen as a special deterministic case; when $b \to \infty$, $J(t) \to 1 - \rho\ \exp(-\lambda t)$ and $\Psi(t) \to \lambda$. Kirkwood considered a further elaboration of Equation (3) by assuming only a fraction of the tags, δ, will have a nonzero probability of shedding; the remainder are regarded as permanently attached. In this event the expected probability of shedding by time t is

$$J(t) = \delta\left[1 - \rho\left(\frac{b}{b + \lambda t}\right)^{\mathrm{b}}\right]. \qquad (4)$$

While this approach significantly advances the realism and flexibility of tag-shedding theory, it fails to account for the apparent increase in average shedding rate as observed in the Atlantic bluefin tuna. Thus, although permitting variation in shedding rate among tags, it still considers the rate for each tag to be constant over time.

This condition is not apt to hold. As Kirkwood (1981) himself pointed out, plastic dart tags may become so firmly imbedded and overgrown by tissue as time passes that the probability of shedding approaches zero. This is most apt to occur in species which grow slowly, such as the southern bluefin tuna. On the other hand, it is well known that various metallic tags may corrode with time and their shedding probabilities increase. Plastic tags also deteriorate.

Accordingly, consider the Type II shedding rate to be a function of time, $L(t)$. A relatively simple model for this situation is $L(t) = \alpha + \beta t^{(\gamma-1)}$, permitting a wide variety of forms for the instantaneous shedding process. In general, all three parameters of this model could be specified as random variables. Thus with $\alpha > 0$, $\beta > 0$, and $-\infty < \gamma < \infty$ the probability of shedding might increase over time for some fish in a cohort, decrease for others, and be constant for the remainder. However, to simplify the analysis assume here that γ is fixed and identical for all members of the cohort. Now if α and β are independently distributed as gamma random variables we have

$$J(t) = \delta\left[1 - \rho\left(\frac{b}{b + \lambda t}\right)^{\mathrm{b}}\left(\frac{\gamma c}{\gamma c + \xi t^{\gamma}}\right)^{\mathrm{c}}\right] \qquad (5)$$

and

$$\Psi(t) = \left(\frac{b\lambda}{b + \lambda t}\right) + \left(\frac{\gamma c\ \xi t^{\gamma-1}}{\gamma c + \xi t^{\gamma}}\right)$$

where the new symbols are ξ, the expected value of β, and c, the reciprocal of the squared coefficient of variation of β. Hence, if between-tag variability in α and β approaches zero,

$$J(t) \to \delta\left\{1 - \rho\ \exp\left[-\left(\frac{\lambda t + \xi t^{\gamma}}{\gamma}\right)\right]\right\}$$

and $\Psi(t) \to \lambda + \xi t^{(\gamma-1)}$. In the basic model at Equation (4), for tags still in place at time t the conditional probability of shedding in the interval $(t, t + dt)$ is independent of t. In the extended model at Equation (5), this conditional probability may also increase or decrease with t depending on γ.

While elaboration of the tag-shedding equations in this manner is straightforward, it is doubtful whether a very clear discrimination between such parameter-laden models is possible given the usual recapture statistics. Distinctions between the extended models are reduced by the integration of the shedding processes over several recapture periods and are further obscured by sampling variation.

However, on the basis of these conceptual models of the tag-shedding process we can now write the well-known equations describing the expected number of tags of a specified type still attached at time t. For $N_d(0)$ fish initially double-tagged with Types A and B tags, let

$$S(t) = \pi \cdot \exp\left(-\int_0^t Z(u)du\right)$$

be the probability of survival to time t, where $1 - \pi$ = probability of immediate mortality and $Z(u) = H(u) - L(u)$ is the time dependent instantaneous death rate. Then the expected number of fish bearing a single tag of Type A at time t is $N_A(t) = N_d(0)\ S(t)\ J_B(t)(1 - J_A(t))$. An analogous expression may be written for $N_B(t)$, and if the two tags are considered identical, the subscripts A and B may be dropped to yield

$$N_s(t) = N_A(t) + N_B(t)$$

$$= 2N_d(0)\ S(t)\ J(t)\ (1 - J(t)),$$

the expected number of fish still bearing a single tag at time t.

The expected number of double-tagged fish at time t when A and B types are differentiated is $N_d(t) = N_d(0)\ S(t)(1 - J_A(t))(1 - J_B(t))$ or when no distinction is made between A and B types, $N_d(t) = N_d(0)\ S(t)(1 - J(t))^2$. In any event, the total number of fish expected at time t with one or two tags remaining is $N_{\cdot}(t) = N_s(t) + N_d(t)$.

The processes described above are not directly observable, so inferences about the shedding rates must be made on the basis of catch statistics. When recapture effort is exerted during a time interval we assume it is applied continuously. During a period of length Δ_i beginning at time t_i the expected number of recaptures of tagged fish in category j is therefore

$$E(r_{ji}) = \int_{t_i}^{t_i+\Delta_i} F(u)\ N_j(u)\ du \qquad (6)$$

where $j = A, B, s, d, \cdot$.

To complete the integral at Equation (6) it has been customary to make two key assumptions at this juncture (Chapman et al. 1965). First, we assume the fishing mortality rate, $F(u)$, is a step function constant within each recapture interval, i.e., $F(u) = F_i$ for $t_i < u < t_i + \Delta_i$ Second, we assume the average value of $N_j(u)$ during the interval is approximately equal to $N_j(t_i + \Delta_i/2)$. [This approximation is generally quite good for Δ_i of 1 yr or less. If $N_j(u)$ is linear over the interval the relation is exact regardless of Δ_i.] Under these conditions the set of recapture equations becomes

$$E(r_{ji}) = F_i\ \Delta_i\ N_j(\tau_i) \qquad (7)$$

where $\tau_i = t_i + \Delta_i/2$.

The standard procedures for estimating shedding rate parameters, and many of those to be described shortly, rely on a sequence of ratios of the estimated or observed number of recaptures from the various categories during successive fishing periods. It is clear from the equations above that such ratios will be functions of τ_i and the shedding parameters only, and independent of F_i, $N_d(0)$ and any parameters of the survival function $S(\tau_i)$.

Further, the ratios will be unaffected by nonrecovery or nonreturn as long as these processes operate at constant levels with respect to recaptures during a given time interval and at the same rates for each tagged fish category. Throughout this paper we assume this is so. However, this latter condition is one which could be violated easily, particularly if catches are not inspected carefully for tag recaptures. Where fish are handled individually there may be no difference in recovery rates between single- and double-tagged fish. Otherwise, recovery rates may be greater in double-tagged individuals. Once tagged fish are recovered, there may be further problems with respect to return rates. Laurs et al. (1976) in a study of shedding rates in North Pacific albacore, *T. alalunga*, and Myhre (1966) in experiments with Pacific halibut, *Hippoglossus stenolepis*, allowed for the possibility that a certain proportion of double-tagged recoveries would be misreported as having only a single tag. [For example, a fisherman might pocket one of the tags as a souvenir, or one tag might be simply lost after recapture.]

ESTIMATION OF SHEDDING RATES AND PARAMETERS

In the analysis of tag-shedding data a broad range of objectives may be pursued, and these give rise to a variety of estimation problems and approaches. Fundamentally, of course, the analyst wishes to correct systematic bias in estimates of basic population parameters caused by tag loss. There are several ways to do this. Where concurrent single-tagging and double-tagging experiments are conducted, information on shedding rates from the double-tagging may be used to compute adjustment factors, which in turn are applied to recoveries from the primary single-tagging study. Thus in single-tag estimation procedures based on Equation (1), for example, r_i would simply be replaced by

$$r_i' = r_i \ \kappa_i^{-1}, \tag{8}$$

where κ_i, estimated from double-tagging, is the probability that a tag will still be attached at time τ_i. If returns from the double-tagging experiment are too few to provide an estimate of κ_i for each recapture interval, interpolation is necessary. In any event, in this approach only minimal assumptions need be made about the manner in which shedding occurs.

In most treatments of tag shedding, however, a specific model is postulated for the shedding process. Once the parameters of such a model are estimated, appropriate adjustments for tag shedding are made either to the single-tag recovery data, as above, or directly to estimated population parameters. A third strategy is to conduct the experiment entirely with double-tagged fish, and to estimate mortality rates and other population parameters directly, in such a way that no corrections are necessary.

These various approaches are discussed now in greater detail, assuming a continuous recapture process. For situations in which tagged fish are recaptured once at most, but only in point samples, some estimation procedures are given by Seber (1973) and Seber and Felton (1981). For multiple-recapture models of the Jolly-Seber type, again with point sampling, the reader should consult Arnason and Mills (1981).

Estimating Adjustment Factors for Single-Tag Recoveries

Here we estimate κ_i, the probability of tag retention at time τ_i, the midpoint of the ith recapture period. We assume the shedding probabilities for each tag are identical and independent of the status of the other tag, and that recovery and reporting rates are the same for recaptured fish bearing either one tag or two. Under these conditions the number of double-tag recoveries, r_{di}, is proportional to κ_i^2 and the number recovered with only a single tag remaining, r_{si}, is proportional by the same factor to $2\kappa_i(1-\kappa_i)$. Of the total number of recoveries from the double-tagging experiment in the ith period, the proportion bearing two tags is therefore

$$P_{di} = \frac{\kappa_i}{2 - \kappa_i} .$$

Maximum likelihood (ML) estimates of the κ_i are now easily derived. We assume the conditional distribution of r_{di}, given $(r_{di} + r_{si})$, is binomial with parameter P_{di}. The likelihood of the ith recapture sample is thus

$$\mathfrak{L}_i = \left(\frac{r_{\cdot i}!}{r_{di}! \ r_{si}!}\right)\left(\frac{\kappa_i}{2-\kappa_i}\right)^{r_{di}}\left(1 - \frac{\kappa_i}{2-\kappa_i}\right)^{r_{si}} .$$

The ML estimator of κ_i is easily found:

$$\hat{\kappa}_i = \frac{2r_{di}}{r_{si} + 2r_{di}} . \tag{9}$$

This result is also given by Seber (1973) under somewhat different assumptions. The asymptotic variance of $\hat{\kappa}_i$ is

$$\sigma^2_{\hat{\kappa}_i} = \frac{\kappa_i(1-\kappa_i)\,(2-\kappa_i)^2}{2r_{\cdot i}} . \tag{10}$$

As usual, numerical estimates are computed by inserting $\hat{\kappa}_i$ in place of κ_i.

Note that $\hat{\kappa}_i$ has a small negative statistical bias. In fact, using a Taylor series expansion it may be shown that

$$E(\hat{\kappa}_i) \simeq \kappa_i \left[1 - \frac{(1-\kappa_i)\,(2-\kappa_i)}{2r_{\cdot i}}\right].$$

Bias increases with time out, i.e., as κ_i decreases, and is inversely related to the total number of recaptures. When $\kappa_i = 0.5$ and $r_{\cdot i} = 10$, the negative bias in $\hat{\kappa}_i$ is <4%.

Note further that since the likelihood function is conditioned on $r_{\cdot i}$, inferences based on Equations (9) and (10) apply strictly only to the particular experimental outcome being studied, and not to the broader class of results which might be obtained in replications of the experiment. Providing that the approximation in Equation (7) is valid, a more complicated unconditional model would yield the same estimate of κ_i, but the variance of $\hat{\kappa}_i$ would be greater, reflecting the stochastic nature of the mortality and recapture processes which lead to the $r_{\cdot i}$. Since our interest is in estimating shedding rates and not mortality rates, as a rule we consider only the simpler conditional likelihoods.

Above we have assumed the two tags are identical insofar as shedding rates are concerned. When they are subject to different shedding rates another set of estimators is required. Where A and B tags are identified, the number of A-type recaptures, r_{Ai}, is proportional to $\kappa_{Ai}(1-\kappa_{Bi})$ while r_{Bi} is proportional to $\kappa_{Bi}(1-\kappa_{Ai})$. The number of double-tagged recaptures is proportional to $\kappa_{Ai}\,\kappa_{Bi}$. We assume the number of recaptures in the three classes are trinomial given $r_{Ai} + r_{Bi} + r_{di}$, with conditional probabilities

$$P_{Ai} = \frac{\kappa_{Ai}(1 - \kappa_{Bi})}{1 - (1 - \kappa_{Ai})\,(1 - \kappa_{Bi})}$$

$$P_{Bi} = \frac{\kappa_{Bi}(1 - \kappa_{Ai})}{1 - (1 - \kappa_{Ai})\,(1 - \kappa_{Bi})}$$

$$P_{di} = \frac{\kappa_{Ai}\,\kappa_{Bi}}{1 - (1 - \kappa_{Ai})\,(1 - \kappa_{Bi})}\,.$$

These assumptions lead to the *ML* estimates

$$\hat{\kappa}_{Ai} = \frac{r_{di}}{r_{Bi} + r_{di}} \quad \text{and} \quad \hat{\kappa}_{Bi} = \frac{r_{di}}{r_{Ai} + r_{di}}\,.$$

Estimating Parameters of Specific Models

Regression Methods

Despite the directness and simplicity of the general adjustment procedure outlined above, most double-tag analyses have aimed at unraveling specific underlying mechanisms of the tag-shedding process. The probability of tag retention, κ_i, is then seen as a continuous function of time and a vector of model parameters, θ, to be estimated from the recapture data. In the terminology established above, $\kappa_i = 1 - J(\tau_i)$. Thus if $\hat{\kappa}_i$ or some transformation of $\hat{\kappa}_i$ is plotted against τ_i the form of an appropriate shedding model may be revealed. In fact, this is the approach adopted in much of the recent tag-shedding literature, and various weighted regression procedures have been developed to handle the parameter estimation. The general formulation of these is: find θ such that

$$S(\theta) = \sum_{i=1}^{n} w_i\,(y_i - f_i(\theta))^2$$

is minimum. In the two-parameter Bayliff-Mobrand model $y_i = \ln\hat{\kappa}_i$, where $\hat{\kappa}_i$ is given in Equation (9), and $f_i(\theta) = \ln\rho - L\tau_i$. In the four-parameter Kirkwood model

$$y_i = 1 - \hat{\kappa}_i$$

and

$$f_i(\theta) = \delta\left\{1 - \rho\left(\frac{b}{b + \lambda\tau_i}\right)^b\right\}.$$

In both cases the authors suggest setting $w_i = r_{\cdot i}$. This is not optimal in a statistical sense, but is clearly preferable to equal weighting. It should be noted further that neither the Bayliff-Mobrand model nor the Kirkwood model is based on an explicit consideration of error structure for the observations. For example, there is considerable support in the literature for a multiplicative error in the recapture process, i.e., $r_{si} = E(r_{si})\exp(\epsilon_{si})$ and $r_{di} = E(r_{di})\exp(\epsilon_{di})$ and in this case the algebra leads one to the nonlinear model

$$\ln\left\{\frac{r_{si}}{2r_{di}}\right\} = \ln\left\{\frac{J(\tau_i)}{1 - J(\tau_i)}\right\} + \epsilon_i$$

where ϵ_i has mean 0 and variance $\sigma^2_{\epsilon_i}$. Appropriate weights for this model are

$$w_i = \sigma^{-2}_{\epsilon_i} \simeq \frac{r_{si}\,r_{di}}{r_{\cdot i}}\,.$$

The regression models discussed here have assumed that recaptures are obtained from a single cohort of tagged fish. However, it is often the case that several lots of tagged fish are released at different times, so the recaptures in a particular interval may come from different cohorts. In this event the analysis may be applied to each of the m cohorts separately, provided these are fairly large. When multiple releases are made but the individual cohorts are small, so that relatively few recaptures are expected from each cohort, the usual procedure is to assume mortality rates and shedding rates are constant and identical for each group and to simply aggregate the recapture statistics from the several releases. Let the recapture intervals be of equal length, Δ, and let r_{sij} and r_{dij} denote the number of single-tagged and double-tagged fish from the jth cohort recaptured during the ith interval following that cohort's liberation. Employing the Bayliff-Mobrand linear regression model, one can estimate $\ln\rho$ and L in the usual manner as

$$\hat{\beta} = (X^T\,W\,X)^{-1}\,X^T\,W\,Y \qquad (11)$$

where $\beta = [\ln\rho \;\; L]^T$
$X = \{x_{ij}\}$ is the augmented data matrix

such that $x_{i1} = 1$ for all i and $x_{i2} = -(i - 1/2)\,\Delta$

$Y = \{y_i\}$ is the vector of dependent variables with elements

$$y_i = \ln\left\{\frac{2\sum_{j=1}^{m_i} r_{dij}}{\sum_{j=1}^{m_i} r_{sij} + 2\sum_{j=1}^{m_i} r_{dij}}\right\}. \qquad (12)$$

Here W is a matrix of statistical weights, and m_i is the number of cohorts for which recapture statistics are available in the ith postrelease interval. The symbol T denotes the matrix transpose.

If sufficient recaptures are obtained to analyze each cohort separately (say $r_{ij} \geq 10$) but a common shedding rate is assumed, several alternative approaches are available. First we can treat the separate releases as partial replicates of the same experiment and construct the dependent variables as the logarithms of the geometric means of individual statistics for each cohort. Thus to estimate $\ln\rho$ and L we use Equation (11) as before but now set

$$y_i = \sum_{j=1}^{m_i} \ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right)\Big/ m_i. \qquad (13)$$

Although as an estimator of $\ln\hat{\kappa}_i$ Equation (13) usually has slightly greater negative bias than Equation (12), such bias is negligible and the approach taken in Equation (13) has the advantage that statistical weights may be calculated empirically for cases where $m_i \geq 2$. In particular, define the ith diagonal element of W as

$$w_{ii} = m_i(m_i - 1)\left[\sum_{j=1}^{m_i}\left(\ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right) - y_i\right)^2\right]^{-1}$$

where y_i is given by Equation (13), and let $w_{ij} = 0$ for $i \neq j$. When some of the m_i are equal to 1, then the w_{ii} may be computed using the delta method as

$$w_{ii} = m_i^2\left[\sum_{j=1}^{m_i}\left(\frac{r_{sij}(r_{sij} + r_{dij})}{r_{dij}(r_{sij} + 2r_{dij})^2}\right)\right]^{-1}$$

on the assumption that the r_{dij} and r_{sij} are complementary binomial variables.

A second approach when the shedding rates are constant and the r_{ij} are sufficiently large is to treat returns from each of the m releases separately and then average the individual estimates. Thus the overall estimate of L, for example, would be

$$\hat{L} = \sum_{j=1}^{m} w_j' \, \hat{L}_j$$

where $\hat{L}_j$ is the estimated slope from the linear regression of

$$y_{ij} = \ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right)$$

on τ_i. Here the individual estimate of L from the jth cohort is given a weight w_j' inversely proportional to its relative variance. In practice we substitute the statistic

$$\hat{w}_j' = \frac{\hat{\sigma}^{-2}_{\hat{L}_j}}{\sum_{j=1}^{m} \hat{\sigma}^{-2}_{\hat{L}_j}},$$

$\hat{\sigma}^{-2}_{\hat{L}_j}$ being the estimated variance of L_j computed in the jth regression. For the regression analysis itself, appropriate statistical weights for the y_{ij} would be proportional to

$$\hat{\sigma}^{-2}_{y_{ij}} = \frac{r_{dij}\,(r_{sij} + 2r_{dij})^2}{r_{sij}\,(r_{sij} + r_{dij})}.$$

Finally, the variance of $\hat{L}$ may be estimated as

$$\hat{\sigma}^2_{\hat{L}} = \sum_{j=1}^{m} \hat{w}_j'^2\, \hat{\sigma}^2_{\hat{L}_j} = \left[\sum_{j=1}^{m} \hat{\sigma}^{-2}_{\hat{L}_j}\right]^{-1}.$$

A third approach is to assume that the set of regression estimates from the m cohorts are sampled from an underlying but unspecified stochastic process which, with respect to the estimation of Type II shedding rate, has mean L and variance $\sigma^2_{\hat{L}}$. The regressions of y_{ij} on τ_i are unweighted, and empirical estimates of L and $\sigma^2_{\hat{L}}$ are given very simply by

$$\hat{L} = \sum_{j=1}^{m} \hat{L}_j \Big/ m$$

and

$$\hat{\sigma}^2_{\hat{L}} = \sum_{j=1}^{m} (\hat{L}_j - \hat{L})^2 \Big/ m(m - 1),$$

where $\hat{L}_j$ is the regression estimate corresponding to the jth cohort.

A shortcoming of many double-tag analyses is that attention has been focused on estimating constant ρ and L despite the existence of multiple-release statistics. In fact the multiple-release experiment permits a more elaborate assessment of shedding processes, with the level of detail determined by specific characteristics of the experimental design. To illustrate this, consider an experiment with six recapture periods of equal length, Δ. Two cohorts of double-tagged fish are released, at the beginning of the first and fourth periods. We assume there is a unique Type I shedding rate associated with each cohort, and that the Type II shedding rate is the same for each group but is a function of time following release. Specifically, we assume the latter rate is constant for two recapture intervals following the release of any cohort, may then change to another constant level for two more periods, and so on.

The recapture statistics from the experiment may be arrayed as follows:

	Recapture interval:					
Release group	*1*	*2*	*3*	*4*	*5*	*6*
1	r_{s11}	r_{s12}	r_{s13}	r_{s14}	r_{s15}	r_{s16}
	r_{d11}	r_{d12}	r_{d13}	r_{d14}	r_{d15}	r_{d16}
2				r_{s21}	r_{s22}	r_{s23}
				r_{d21}	r_{d22}	r_{d23}

Note that $m_1 = m_2 = m_3 = 2$ and $m_4 = m_5 = m_6 = 1$.

The parameter vector $\beta = [\ln\rho_1 \ln\rho_2 L_1 L_2 L_3]^T$ may now be estimated from Equation (11) with Y as given in Equation (13) and the data matrix defined as

$$X = \begin{bmatrix} 1/2 & 1/2 & -\Delta/2 & 0 & 0 \\ 1/2 & 1/2 & -3\Delta/2 & 0 & 0 \\ 1/2 & 1/2 & -2\Delta & -\Delta/2 & 0 \\ 1 & 0 & -2\Delta & -3\Delta/2 & 0 \\ 1 & 0 & -2\Delta & -2\Delta & -\Delta/2 \\ 1 & 0 & -2\Delta & -2\Delta & -3\Delta/2 \end{bmatrix}.$$

As usual, the covariance matrix of $\hat{\beta}$ is estimated by $\hat{V} = (X^T W X)^{-1}$.

With a little imagination this general linear model can easily be adapted to accommodate a wide variety of multiple-release experimental designs. Standard analysis of covariance techniques may be applied to test the associated hypotheses concerning β.

Maximum Likelihood Methods

As an alternative to the least squares methods we now describe some ML procedures for estimating the model parameters in the single-release case. Given the total number of recaptures in the ith period we again assume the numbers falling in the various classes are multinomially distributed. Thus when the A and B tags are identical there are just two classes, and the numbers in each are binomial variables with conditional expectations

$$\begin{aligned} E(r_{di}) &= r_{\cdot i} \quad P_{di} \\ &= r_{\cdot i}\left\{\frac{1 - J(\tau_i)}{1 + J(\tau_i)}\right\} \\ &= r_{\cdot i}\left\{\frac{[1 - J(\tau_i)]^2}{1 - J(\tau_i)^2}\right\} \end{aligned}$$

and $E(r_{si}) = r_{\cdot i}\,(1 - P_{di})$. Assuming further that the statistics for successive periods are mutually independent, the joint likelihood function for the double-tag recovery data $\{r_{d1}\ r_{d2}, \ldots, r_{dn}\}$ given $\{r_{\cdot 1}, r_{\cdot 2}, \ldots, r_{\cdot n}\}$ is

$$\mathfrak{L} = \prod_{i=1}^{n} \left(\frac{r_{\cdot i}!}{r_{di}!\ r_{si}!}\right) P_{di}^{\ r_{di}} (1 - P_{di})^{r_{si}} \qquad (14)$$

where P_{di} is a function of τ_i and the vector of parameters to be estimated, θ.

When the A and B tags are not identical, the recaptures are partitioned into three disjoint classes, and the numbers in each are trinomial with expectations

$$E(r_{Ai}) = \frac{J_B(\tau_i)\ (1 - J_A(\tau_i))}{1 - J_B(\tau_i)\ J_A(\tau_i)}\ r_{\cdot i} = r_{\cdot i}\ P_{Ai}$$

$$E(r_{Bi}) = \frac{J_A(\tau_i)\ (1 - J_B(\tau_i))}{1 - J_B(\tau_i)\ J_A(\tau_i)}\ r_{\cdot i} = r_{\cdot i}\ P_{Bi}$$

and

$$\begin{aligned} E(r_{di}) &= \frac{(1 - J_A(\tau_i))\ (1 - J_B(\tau_i))}{1 - J_B(\tau_i)\ J_A(\tau_i)}\ r_{\cdot i} \\ &= r_{\cdot i}\ (1 - P_{Ai} - P_{Bi}). \end{aligned}$$

Now the joint conditional likelihood of the recapture sample is

$$\mathcal{L} = \prod_{i=1}^{n} \left(\frac{r_i!}{r_{Ai}!\; r_{Bi}!\; r_{di}!} \right) P_{Ai}^{\,r_{Ai}}\, P_{Bi}^{\,r_{Bi}} \times (1 - P_{Ai} - P_{Bi})^{r_{di}}.$$

In either case, once the underlying model and the corresponding elements of θ are identified, the ML estimates of θ may be computed by maximizing $\mathcal{L}$ directly using a variety of iterative search procedures. In some situations the derivatives of $\mathcal{L}$ with respect to θ are easily derived, but even then only numerical solutions are possible.

For example, when A and B tags are identical and $J(\tau_i) = 1 - \rho(\exp(-L\tau_i))$, the ML estimates of ρ and L are found by solving the system of equations

$$0 = \sum_{i=1}^{n} \tau_i C_i \quad \text{and} \quad 0 = \sum_{i=1}^{n} C_i$$

$$\text{where } C_i = \frac{(1 + P_{di})(r_{di} - P_{di}\, r_i)}{1 - P_{di}}$$

$$= J(\tau_i)^{-1} \left\{ r_{di} - r_i \left(\frac{1 - J(\tau_i)}{1 + J(\tau_i)} \right) \right\}$$

$$= J(\tau_i)^{-1} \{ r_{di} - E(r_{di}) \}.$$

The asymptotic covariance matrix of $\hat{L}$ and $\hat{\rho}$ may then be derived in the usual manner by inverting the corresponding negative information matrix

$$I = \begin{bmatrix} \sum_{i=1}^{n} \tau_i^2 D_i & -\frac{1}{\rho} \sum_{i=1}^{n} \tau_i D_i \\ -\frac{1}{\rho} \sum_{i=1}^{n} \tau_i D_i & \frac{1}{\rho^2} \sum_{i=1}^{n} D_i \end{bmatrix}$$

$$\text{where } D_i = \frac{r_i\, P_{di}\, (1 + P_{di})^2}{1 - P_{di}} .$$

Explicit analytical solutions are possible when there is only a single recapture period centered at τ and the model is reduced to a one-parameter function of either the Type I or Type II shedding rate, i.e., either $J(\tau) = 1 - \exp(-L\tau)$ or $J(\tau) = 1 - \rho$. In this event the ML estimate of L (with $\rho = 1$) is

$$\hat{L} = -\frac{1}{\tau} \ln \left\{ \frac{2r_d}{r_s + 2r_d} \right\} \qquad (15)$$

with asymptotic variance estimated by

$$\hat{\sigma}^2_{\hat{L}} = \frac{r_s\,(r_s + r_d)}{\tau^2 r_d\,(r_s + 2r_d)^2} ,$$

or when shedding is a function of ρ only (with $L = 0$)

$$\hat{\rho} = \frac{2r_d}{r_s + 2r_d} \qquad (16)$$

and

$$\hat{\sigma}^2_{\hat{\rho}} = \frac{r_s\, 2r_d}{(r_s + 2r_d)^3} .$$

In the case of identical A and B tags a convenient alternative to direct maximization of the likelihood function is to fit the recapture data to their expectations using an iteratively reweighted Gauss-Newton algorithm. To accomplish this one may use routines available in certain standard statistical software packages, e.g., BMDP[2]. Specifically, we find an admissible value of θ which minimizes the sum of squares

$$S' = \sum_{i=1}^{n} w_i [r_{di} - E(r_{di})]^2.$$

Since the r_{di} are assumed to be binomial (i.e., of "regular exponential" form), minimizing S' with a Gauss-Newton routine is equivalent to maximizing the likelihood of Equation (14) provided the weights used are the reciprocals of the variances of the r_{di} and are recomputed at each iteration based on the current parameter values (Wedderburn 1974; Jennrich and Moore 1975; Jennrich and Ralston 1978). In this case the weights must be $\tilde{w}_i = [r_{\cdot i}\, \tilde{P}_{di}\,(1 - \tilde{P}_{di})]^{-1}$, where $\tilde{P}_{di}$ is the function P_{di} evaluated at the current parameter estimates. Asymptotic standard errors for the parameter estimates are also computed by the BMDP routine.

A similar device may be used when a distinction is made between A and B tags. Given $r_{Ai} + r_{di}$ we assume r_{di} is binomial with expectation $E_B(r_{di}) = (r_{Ai} + r_{di})\,(1 - J_B(\tau_i))$. Analogously,

---

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

$E_{\mathrm{A}}(r_{di}) = (r_{\mathrm{B}i} + r_{di})\,(1 - J_{\mathrm{A}}(\tau_i))$. Thus an iteratively reweighted Gauss-Newton algorithm minimizing

$$S'_{\mathrm{B}} = \sum_{i=1}^{n} w_{\mathrm{B}i}\,(r_{di} - E_{\mathrm{B}}(r_{di}))^2$$

with $w_{\mathrm{B}i} = \tilde{w}_{\mathrm{B}i} = [(r_{\mathrm{A}i} + r_{di})\,\tilde{J}_{\mathrm{B}}(\tau_i)(1 - \tilde{J}_{\mathrm{B}}(\tau_i))]^{-1}$ is used to compute *ML* estimates of shedding parameters for the B class of tags. A parallel procedure gives *ML* estimates of parameters for the A class. Note that the two sets of parameter estimates are not independent.

Unknown Recapture Times

A tacit assumption in the foregoing procedures is that the time between release and recapture for each returned fish is known to "interval accuracy," and that exact recapture time information is available for only a fraction of the recoveries, so that all recoveries are grouped into the n time intervals to permit estimation. This will often be the case. However, in some fisheries it is conceivable that only the crudest sort of information is available on recapture times. For estimation purposes, all that is known is r_d and r_s, the total number of recaptures in each class over the experimental period $(0, T)$. When T is relatively small, say 1 yr or less, then estimation of a single Type I or Type II shedding parameter is possible, as in Equation (15) or (16). In an experiment of longer duration this is not feasible. However, it is possible under certain circumstances to estimate the ratio of the Type II shedding rate to other Type II losses. Let fishing be constant, continuous, and uniform at an instantaneous rate F. Assume further that the total instantaneous mortality rate is a constant, Z, and that shedding of tags occurs at an instantaneous rate L. If there are no Type I losses, the ratio of $E(r_s)$ to $E(r_d)$ in a double-tagging experiment approaches

$$x = \frac{2L}{Z + L}$$

as $T \to \infty$. Thus if $L = aZ$, a moment estimator of a is provided by

$$\begin{aligned}\hat{a} &= \frac{\hat{x}}{2 - \hat{x}} \\ &= \frac{r_s}{2r_d - r_s}, \quad 0 \le \frac{r_s}{r_d} < 2 \qquad (17)\end{aligned}$$

and if one has an estimate of Z which has a systematic bias due to Type II shedding, say Z^+, then a corrected estimate may be obtained, i.e., $Z^* = Z^+(1 + \hat{a})^{-1}$.

This method may also be used where single-tagging and double-tagging experiments are run concurrently. Then if $N_d(0)$ fish are released double-tagged and $N_s(0)$ with single tags, let r'_d and r'_s be recaptures from each group still bearing the initial complement of tags. Under the same assumptions as above this leads to

$$\hat{a} = \frac{r'_s N_d(0) - r'_d N_s(0)}{2r'_d N_s(0) - r'_s \mathrm{N}_d(0)}, \quad 1 \le \frac{r'_s N_d(0)}{r'_d N_s(0)} < 2.$$

Exact Recapture Times

Turning now to the other end of the spectrum, under ideal conditions it is possible that the exact time out will be known for each fish returned. When exact recapture times are available for all fish the returns from a single-tagging experiment may be analyzed using *ML* procedures first developed by Gulland (1955) and later elaborated by Chapman (1961) and Paulik (1963). These rest on the assumption of binomial recapture probabilities based on constant Type II loss rates and on a resulting conditional recapture time distribution which is truncated negative exponential. Chapman et al. (1965) extended the same concepts to returns of fish initially double-tagged and still retaining both tags upon recapture, and showed that the difference between the estimated total Type II loss rate in a double-tagging experiment and the corresponding total Type II loss rate in a single-tagging study yielded an estimate of L. They noted that this is the best estimate of L possible using only the recapture information from a single-tagging experiment and from fish put out and returned with two tags. Left open was the possibility of combining this information with recapture times for fish initially double-tagged but returned with only one tag still attached. For this class of fish the distribution of recapture times is more complicated.

We now consider an exact recapture time model for an experiment based exclusively on fish initially double-tagged. Suppose $N'_d(0)$ double-tagged fish are released at time 0. Over the course of the experiment, terminating at time T, a total of r_d fish are recaptured and returned with both tags intact, and r_s with only a single tag remaining. In addition, for each tagged fish returned we assume the exact recapture time is known, i.e., we know $\{t_{s1}, t_{s2}, ..., t_{sr_s}\}$ and $\{t_{d1}, t_{d2}, ..., t_{dr_d}\}$.

Let $\Phi_d = Pr$ {fish is returned with both tags intact in $(0, T)$} and $\Phi_s = Pr$ {fish is returned with one tag remaining in $(0, T)$}. Then, assuming independence between fish and between the two tags initially applied, the numbers of returns in the various classes are trinomial random variables, i.e.,

$$Pr\{r_d, r_s\} = \frac{N_d(0)!}{r_d!\; r_s!\; (N_d(0) - r_d - r_s)!} \times \Phi_s^{r_s}\, \Phi_d^{r_d} (1 - \Phi_s\, \Phi_d)^{N_d(0)-r_s-r_d}.$$

Following principles set out previously we write the recapture probabilities as

$$\Phi_s = 2\int_0^T F(u)\; S(u)\; J(u)\; (1 - J(u))\; du$$

and

$$\Phi_d = \int_0^T F(u)\; S(u)\; (1 - J(u))^2\; du.$$

Further, the conditional probability densities for recapture times are

$$f_s(t) = \begin{cases} 2F(t)\; S(t)\; J(t)(1 - J(t))/\Phi_s & 0 < t < T \\ 0 & \text{otherwise} \end{cases}$$

$$f_d(t) = \begin{cases} F(t)\; S(t)(1 - J(t))^2/\Phi_d & 0 < t < T \\ 0 & \text{otherwise.} \end{cases}$$

The joint likelihood function for the observed numbers of single- and double-tag recoveries and the respective sets of recapture times may now be written as

$$\mathcal{L} = Pr\{r_d, r_s\} \prod_{i=1}^{r_s} f_s(t_{si}) \prod_{i=1}^{rd} f_d(t_{di}).$$

For specified forms of $F(u)$, $S(u)$, and $J(u)$ computation of ML estimates may now be contemplated, although the form of $\mathcal{L}$ is apt to be exceedingly complex in most situations. For example, taking the most elementary case, assume that $J(u) = 1 - \exp(-Lu)$, $S(u) = \exp[-(M + F)u]$ and $F(u) = F$ for $0 < u < T$. Also let $T \to \infty$. Under these conditions the log-likelihood becomes

$$\ln \mathcal{L} = \mathrm{K} + r_.\ \ln F + (N_d(0) - r_.) \times \ln\left(1 - \frac{2LF^2}{(F + M + L)(F + M + 2L)^2}\right) - (F + M)\; T_. - L(T_s + 2T_d) + \sum_{i=1}^{r_s} \ln(1 - \exp(-Lt_{si}))$$

where K is a function of the observations only,

$$T_s = \sum_{i=1}^{r_s} t_{si}, \qquad T_d = \sum_{i=1}^{rd} t_{di},$$

$$T_. = T_s + T_d, \quad \text{and} \quad r_. = r_s + r_d.$$

Using numerical methods this may now be maximized as a function of F, M, and L in the usual manner to yield ML estimates of these parameters, as well as asymptotic variance estimates.

A simpler approach which yields information on $Z = F + M$ and L is to condition the likelihood of r_d and r_s on the total number of recaptures, $r_.$, i.e.,

$$Pr\; \{r_d,\; r_s\} = \left(\frac{r_.!}{r_s!\; r_d!}\right)\left(\frac{\Phi_s}{\Phi_s + \Phi_d}\right)^{r_s}\left(\frac{\Phi_d}{\Phi_s + \Phi_d}\right)^{r_d}.$$

This gives the log-likelihood

$$\ln \mathcal{L} = \mathrm{K}' + r_.\ \{\ln(Z + L) + \ln(Z + 2L) - \ln(Z + 3L)\} - ZT_. - L(T_. + T_d) + \sum_{i=1}^{r_s} \ln(1 - \exp(-Lt_{si})) \qquad (18)$$

where K′ is independent of Z and L.

Differentiating Equation (18) with respect to Z and L and setting the derivatives to zero one finds that the ML estimates of Z and L satisfy, among other relations, the equation

$$\frac{T_.}{r_.} = \frac{1}{Z + L} + \frac{1}{Z + 2L} - \frac{1}{Z + 3L}.$$

Combining this with the result at Equation (17) leads immediately to a solution for $\hat{Z}$, i.e.,

$$\hat{Z} = \frac{r.}{T.}\left[\frac{1}{1+\hat{a}} + \frac{1}{1+2\hat{a}} - \frac{1}{1+3\hat{a}}\right]$$

whence $\hat{L} = \hat{a}\,\hat{Z}$.

Estimating Mortality Rates by Double-Tagging All Fish

In most of the preceding sections we assumed the basic purpose in double-tagging was to provide auxilliary information on shedding rates which could then be applied to correct recapture statistics or mortality rate estimates obtained in a primary single-tagging experiment. An attractive alternative is to use double-tagged fish entirely and to estimate the mortality rates and other vital parameters in such a way that no bias corrections are necessary. If exact recapture times are recorded, the *ML* model just discussed is appropriate. When recapture data are grouped into n time intervals of length Δ_i centered at times τ_i, a convenient context for developing this approach is the single-tagging regression model suggested by Chapman (1961) and discussed further by Cormack (1968) and Seber (1973). This takes the form

$$\ln\left(\frac{r_i}{\mathfrak{f}_i\,\Delta_i}\right) = \ln[q\rho N_s(0)] - q\mathfrak{f}_i' - X\tau_i + e_i \quad (19)$$

where $\mathfrak{f}_i$ = the nominal fishing effort during period i

$\mathfrak{f}_i' = \sum_{j=1}^{i-1} \mathfrak{f}_j\,\Delta_j + \frac{\mathfrak{f}_i\,\Delta_i}{2}$ = the estimated nominal effort up to time τ_i

q = the catchability coefficient

e_i = a random error term.

In this particular model one obtains estimates of q and X, and, since $N_s(0)$ is known, an estimate of ρ as well. However, in the presence of Type II shedding the exploitation rate for any period will be underestimated, i.e., hidden in $\hat{X}$ will be the term L. The usual procedure would be to correct $\hat{X}$ by subtracting $\hat{L}$, where $\hat{L}$ is obtained in an independent double-tagging experiment. Instead, if we apply the model directly to recapture statistics from a double-tagging experiment ($N_d(0)$ fish initially double-tagged) we will obtain an estimate of X unaffected by Type II losses and in need of no corrections. This is accomplished by substituting the dependent variable

$$\ln\left\{\left(\frac{r_{si} + 2r_{di}}{2\Delta_i\,\mathfrak{f}_i}\right)\Big/\left(\frac{2r_{di}}{r_{si} + 2r_{di}}\right)\right\}. \quad (20)$$

Further, it now transpires that the estimate of the regression intercept term is free of Type I shedding effects, i.e., one will estimate $\ln[qN_d(0)]$ rather than $\ln[q\rho N_d(0)]$.

If we assume r_{si} and r_{di} are complementary binomial variables given r_i, and that r_i is Poisson, then approximately correct weights for the regression employing Equation (20) are

$$w_i = \left[\frac{1}{r_i}\left(1 + \frac{r_{si}^{3}}{(r_{si} + 2r_{di})^2\, r_{di}}\right)\right]^{-1}.$$

When effort statistics are not available so that a constant fishing mortality rate must be assumed, or when there is a linear dependence between the two independent variables $\mathfrak{f}_i'$ and τ_i, then separate estimates of q and X are not possible using the single-tag model of Equation (19) unless Type I errors are absent. Nor is ρ estimable. Instead, one may only regress $\ln(r_i/\Delta_i)$ on τ_i to yield estimates of $\ln[\rho F N_s(0)]$ and $(F+X)$. But when the model is applied to a double-tagging experiment under the same restrictions, it is still possible to estimate both q and X unaffected by shedding.

Note that the dependent variable of Equation (20) from the double-tagging experiment is analogous to the one of Equation (19) appropriately corrected for tag shedding, as in Equation (8). In both cases the recaptures r_{di} and r_{si} are assumed to be point samples taken exactly at τ_i. Thus while in the example above $\kappa_i = \rho\exp(-L\tau_i)$, the correction procedure of Equation (8) and the method outlined here are independent of assumptions on the manner of tag shedding (cf. Seber 1973:281), provided the recapture intervals are reasonably small (say 1 yr or less).

SUMMARY AND CONCLUSIONS

The aim of this paper has been to extend the theory and methodology of estimating tag-shedding rates through double-tagging. Attention was focused on the situation most commonly encountered in fishery applications, wherein two identical tags are placed on each member of an experimental cohort, tagged fish are recaptured at most once in a fishery which is essentially continuous, and the time at liberty is known exactly for only a fraction of the recapture sample.

The regression models studied by Chapman et al. (1965), Bayliff and Mobrand (1972), and Kirkwood (1981) were extended to permit the Type II shedding rate for each tagged fish to be a function of time. Both deterministic and stochastic versions were presented and previously published models were shown to be special cases.

If all tags are subject to the risk of shedding, i.e., if $\delta = 1$, and if data are available from several recapture periods, a simple plot of $\ln\hat{\kappa}_i$ against τ_i will reveal whether the average Type II shedding rate, $\Psi(t)$, is constant; if it is, the relationship will be linear. In this event the most parsimonious model consistent with the data will be the deterministic model based on a constant Type II shedding rate, L. In addition, if the points suggest a negative intercept on the ordinate the Type I retention rate, ρ, may be added to the parameter set. One may then carry out the parameter estimation using either the Bayliff-Mobrand linear regression model, or the nonlinear regression of $\ln(r_{si}/2r_{di})$ on τ_i, depending on which error structure is assumed. However, since the plot of $\ln\hat{\kappa}_i$ versus τ_i is approximately linear even with multiplicative error in the recapture process, it probably makes little difference which estimation method is used as long as proper statistical weights are incorporated.

If $\delta = 1$ and the plot of $\ln\hat{\kappa}_i$ versus τ_i is nonlinear, one of the more complicated tag-shedding models is called for. A trend which is concave downward suggests that $\Psi(t)$ is increasing with time and points to the stochastic model of Equation (5) or its deterministic counterpart. On the other hand, upward concavity could be explained either by a model in which the Type II shedding rate decreased with time or by Kirkwood's (1981) hypothesis, or by a combination of the two as in Equation (5).

Another useful diagnostic plot is $1 - \kappa_i$ against τ_i. These are the variables considered in Kirkwood's nonlinear model. When L is constant the plotted points will be traced by a line analogous to a von Bertalanffy growth curve with asymptote δ and location parameter ρ, and they should indicate which of these two parameters to include in the model and how much precision to expect in the resulting estimates. (In passing, it is worth mentioning that if δ is to be estimated jointly with L, a longer experiment is required to ensure high precision in the parameter estimates than if L alone is being estimated.)

The treatment of recaptures from double-tagging experiments with multiple cohorts was discussed in the context of the Bayliff-Mobrand model. Alternative methods of combining information from several cohorts to estimate common shedding parameters were proposed, and a general linear model approach was suggested for situations where more elaborate structural assumptions are made. A full numerical evaluation of these procedures remains to be done.

As an alternative to the least squares regression methods usually employed, some new *ML* procedures were presented. These are more difficult to use than the regression techniques, but offer advantages in some situations. For example, when only two recapture periods are possible one cannot compute the precision of regression estimates in the Bayliff-Mobrand model, but standard errors in the equivalent *ML* model are still estimable. The most promising method for deriving *ML* estimates in the general case may be the iteratively reweighted Gauss-Newton algorithm. Indeed, if one has access to the right computer software (such as the BMDPAR and BMDP3R programs supplied by BMDP) this approach is nearly as easy to use as the simple Bayliff-Mobrand linear regression method. A sensible procedure would be to first study the diagnostic plots suggested above for the regression analysis, and then fit the selected model using an iteratively reweighted least squares algorithm.

The estimation procedures discussed above are applicable when data are grouped by recapture interval. For situations in which the exact time at liberty is known for each recapture an unconditional *ML* model was developed. This may be applied not only to estimate shedding rates but also to estimate mortality rates unaffected by shedding. However, in its general form the likelihood function is rather complicated and only numerical solutions would be possible in most situations. Analytical estimators for L and Z were derived for a simplified conditional likelihood. Besides the more stringent data requirements this model requires the extra assumption of constant mortality rates during the experiment.

In the final section it was shown that through double-tagging it is possible to estimate mortality rates free of tag-shedding biases even when the recapture data are available only to interval-accuracy, and without resort to the usual concurrent single-tagging experiment. The model was developed in the simple context of a fixed Type II shedding rate, but the principle applies to more complicated shedding processes as well. If the burden imposed by the second tag can be neglected, it therefore seems advantageous to double-tag all fish. In any case, when shedding is appreciable the greater overall recovery rates from double-tagging make the exclusive use of double-tagged fish a proposition well worth considering.

LITERATURE CITED

ARNASON, A. N., AND K. H. MILLS.
1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Can. J. Fish. Aquat. Sci. 38:1077-1095.

BAGLIN, R. E., JR., M. I. FARBER, W. H. LENARZ, AND J. M. MASON, JR.
1980. Shedding rates of plastic and metal dart tags from Atlantic bluefin tuna, *Thunnus thynnus*. Fish. Bull., U.S. 78:179-185.

BARTHOLOMEW, D. J.
1973. Stochastic models for social processes. John Wiley & Sons, 411 p.

BAYLIFF, W. H.
1973. Materials and methods for tagging purse seine- and baitboat-caught tunas. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 15:465-503.

BAYLIFF, W. H., AND L. M. MOBRAND.
1972. Estimates of the rates of shedding of dart tags from yellowfin tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 15:439-462.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Mar. Fish. Minist. Agric., Fish. Food. (G.B.), Ser. II, 19, 533 p.

CHAPMAN, D. G.
1961. Statistical problems in dynamics of exploited fisheries populations. Proc. Berkeley Symp. Math. Stat. Probab. 4:153-168.
1969. Statistical problems in the optimum utilization of fisheries resources. Bull. Int. Stat. Inst. 42:268-293.

CHAPMAN, D. G., B. D. FINK, AND E. B. BENNETT.
1965. A method for estimating the rate of shedding of tags from yellowfin tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 10:333-352.

CORMACK, R. M.
1968. The statistics of capture-recapture methods. *In* H. Barnes (editor), Oceanography marine biology annual review 6:455-506. George Allen and Unwin, Ltd., Lond.

GULLAND, J. A.
1955. On the estimation of population parameters from marked members. Biometrika 42:269-270.
1963. On the analysis of double-tagging experiments. Int. Comm. Northwest Atl. Fish. Spec. Publ. 4:228-229.

HYND, J. S.
1969. New evidence on southern bluefin stocks and migrations. Aust. Fish. 28(5):26-30.

JENNRICH, R. I., AND R. H. MOORE.
1975. Maximum likelihood estimation by means of nonlinear least squares. Am. Stat. Assoc. Proc. Stat. Comput. Sect., p. 57-65.

JENNRICH, R. I., AND M. L. RALSTON.
1978. Fitting nonlinear models to data. Health Sci. Comput. Facil., Univ. Calif., Los Angeles, BMDP Tech. Rep. 46, 71 p.

KIRKWOOD, G. P.
1981. Generalized models for the estimation of rates of tag shedding by southern bluefin tuna (*Thunnus maccoyii*). J. Cons. Cons. Inst. Explor. Mer 39:256-260.

LAURS, R. M., W. H. LENARZ, AND R. N. NISHIMOTO.
1976. Estimates of rates of tag shedding by North Pacific albacore, *Thunnus alalunga*. Fish. Bull., U.S. 74:675-678.

MCNOLTY, F., J. DOYLE, AND E. HANSEN.
1980. Properties of the mixed exponential failure process. Technometrics 22:555-565.

MYHRE, R. J.
1966. Loss of tags from Pacific halibut as determined by double-tag experiments. Int. Pac. Halibut Comm. Rep. 41, 31 p.

PAULIK, G. J.
1963. Estimates of mortality rates from tag recoveries. Biometrics 19:28-57.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 382 p.

ROBSON, D. S., AND H. A. REGIER.
1966. Estimates of tag loss from recoveries of fish tagged and permanently marked. Trans. Am. Fish. Soc. 95: 56-59.

SEBER, G. A. F.
1973. The estimation of animal abundance and related parameters. Hafner Press, N.Y., 506 p.

SEBER, G. A. F., AND R. FELTON.
1981. Tag loss and the Petersen mark-recapture experiment. Biometrika 68:211-219.

WEDDERBURN, R. W. M.
1974. Quasi-likelihood functions, generalized linear models, and the Gauss-Newton method. Biometrika 61:439-447.

WETHERALL, J. A., AND M. Y. Y. YONG.
1981. Planning double-tagging experiments. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-13, 44 p.

FOUR NEW SPECIES OF SQUID (OEGOPSIDA: *ENOPLOTEUTHIS*) FROM THE CENTRAL PACIFIC AND A DESCRIPTION OF ADULT *ENOPLOTEUTHIS RETICULATA*

LOURDES ALVINA BURGESS[1]

ABSTRACT

Four new species of *Enoploteuthis* (*E. obliqua*, *E. octolineata*, *E. jonesi*, and *E. higginsi*) are described, illustrated, and compared. Adults of *E. reticulata* Rancurel 1970 are described for the first time. A key for all the species is provided.

Cephalopods are important fisheries resources in the Pacific Ocean. Thus, clarification of cephalopod systematics, particularly from areas where they are not thoroughly known such as the central Pacific, is important. Because enoploteuthid squids are deepwater animals that are not easily accessible or profitable to fish, they are not at present generally exploited commercially. In Toyama Bay, Sea of Japan, however, the enoploteuthid squid *Watasenia scintillans* (Berry 1911) is fished regularly in the spring and early summer when swarms of this species migrate to the surface to spawn (Sasaki 1914).

Cephalopods also play important roles in marine food webs. They are the principal food of many marine mammals, fishes, and some birds. Reintjes and King (1953) found that 26% of the aggregate total volume of the stomach contents of yellowfin tuna, *Thunnus albacares*, captured in the central Pacific consisted of cephalopods. King and Ikehara (1956) showed that as much as 33% of the food of the bigeye tuna, *T. obesus*, were squids, including *Enoploteuthis* sp.

Berry (1914) reported on the cephalopods collected on board the U.S. Fish Commission steamer *Albatross* from the Hawaiian area; the collection included enoploteuthid squids but none of them of the genus *Enoploteuthis*. Species of *Enoploteuthis* from Hawaiian waters and the central Pacific are described here for the first time and compared with all the known species of *Enoploteuthis* in the world.

Four new species of pelagic squids belonging to the genus *Enoploteuthis*, together with some adults of *E. reticulata*, were identified during the examination of the large collection of cephalopods at the Honolulu Laboratory, Southwest Fisheries Center of the National Marine Fisheries Service (NMFS), Honolulu, Hawaii (formerly Bureau of Commercial Fisheries Biological Laboratory, Honolulu).

The squids were taken from various areas of the central Pacific on several research vessels operated by the Honolulu Laboratory from 1953 to 1970. The fishing gear was either a modified Cobb trawl, a 10-ft Isaacs-Kidd trawl, or a Nanaimo trawl. The depth of fishing generally was between 50 and 100 m; most of the fishing was done at night.

Details on the capture of the cephalopods reported on here, including all holotypes and paratypes, are available from the original cruise reports and logs on file at the Honolulu Laboratory.

Type specimens are deposited in the cephalopod collections of the Division of Mollusks, U.S. National Museum of Natural History (USNM), Smithsonian Institution.

The terminology of the anatomical parts, measurements, and indices conform to those generally used for squids and in particular to those listed and defined by Roper (1966): ML = mantle length, CH = club hooks, CS = club suckers, MWI = mantle width index, HWI = head width index, FLI = fin length index, FWI = fin width index, ALI = arm length index, and TLI = tentacle length index. As in Roper (1966) the arm length is measured from the first basal hook (or sucker) to the tip of the arm.

The ranges and means of indices given in the descriptions were computed from measurements of the male and female specimens listed in Tables 1 to 5. This is not applicable to indices in-

---

[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii; present address: T. F. H. Publications, Inc., 211 West Sylvania Avenue, Neptune, NJ 07753.

Manuscript accepted April 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

cluded in the remarks on immature individuals; not all their measurements are presented in the tables.

The following abbreviations which appear in the list of material refer to the research vessels: HMS = *Hugh M. Smith*, CHG = *Charles H. Gilbert*, and TC = *Townsend Cromwell*. A + sign after numbers in the text and tables indicates a missing mantle or arm tip, or lost suckers.

FAMILY ENOPLOTEUTHIDAE PFEFFER 1900

Genus *Enoploteuthis* Orbigny 1848

Diagnosis: Enoploteuthids with numerous light organs on mantle, head, and arms; single row of small light organs on ventral surface of eyeball; two rows of hooks on tentacular club; buccal connectives DDVD[2]; fins lateral; and mantle projecting posteriorly as free "tail."

Type species: *Loligo leptura* Leach 1817; Hoyle 1910:409, by elimination.

Enoploteuthis obliqua n. sp.
(Figs. 1, 2A; Table 1)

Enoploteuthis sp. (No. 2), Okutani 1974: figures 12c, d, f.

Holotype: Male, ML 55 mm, TC-48, Stn. 11, 11°47′N, 144°47′W, 31 March-1 April 1970, 50 m, USNM 729722.

Paratypes: 1 female, ML 50 mm, TC-46, Stn. 9, 11°49′N, 144°51′W, 14 October 1969, 50 m, USNM 577605. 1 male, ML 41 mm, TC-46, Stn. 9, 11°49′N, 144°51′W, 14 October 1969, 50 m, USNM 729713. 1 male, ML 58 mm, TC-48, Stn. 19, 11°34′N, 144°54′W, 3-4 April 1970, 50 m, USNM 729688.

Other material: 5 specimens, ML 12-17 mm, TC-43, Stn. 10, 12°03′N, 144°55′W, 8 May 1969, 50 m. 16 specimens, ML 5-18 mm, TC-43, Stn. 14, 11°56′N, 144°56′W, 10 May 1969, 50 m. 5 specimens, ML 12-17 mm, TC-43, Stn. 22, 07°41′N, 145°01′W, 13 May 1969, 50 m. 1 female (from *Alepisaurus* stomach contents), ML 50 mm, TC-44, equatorial central Pacific, July-August 1969, 10-100 m, USNM 729716. 2 specimens, ML 5 and 10 mm, TC-44, Stn. 16, 11°51′N, 144°41′W, 11 July 1969, surface. 1 specimen (from *Alepisaurus* stomach contents), ML 27 mm, TC-44, Stn. 17, 11°N, 144°W, 10 July 1969. 2 specimens, ML 12 and 17 mm, TC-44, Stn. 18, 11°53.2′N, 144°49.3′W, 11 July 1969, 100 m. 1 male, ML 37+ mm, 4 specimens, ML 12-20 mm, TC-44, Stn. 24, 07°32.9′N, 145°58′W, 13 July 1969, 50 m. 1 specimen, ML 13 mm, TC-44, Stn. 32, 07°31.5′N, 144°50.2′W, 17 July 1969, 50 m. 1 specimen, ML 12 mm, TC-44, Stn. 54, 00°01.8′N, 145°08.8′W, 28 July 1969, 50 m. 4 specimens, ML 6-11 mm, TC-47, Stn. 16, 12°02′N, 144°54′W, 23 January 1970, 50 m. 3 specimens, ML 7-10 mm, TC-48, Stn. 16, 11°45′N, 144°46′W, 2-3 April 1970, 20 m. 1 female, ML 40+ mm, TC-48, Stn. 19, 11°34′N, 144°54′W, 3-4 April 1970, 50 m.

Description: The mantle is muscular except for the thin-walled posterior end (tail) consisting of a gelatinous alveolar material. The mantle is widest (MWI 29.1-*32.4*-34.1) at the anterior edge and tapers into a blunt end. The anterior ventral margin is slightly excavated forming low, pointed lateral angles on each side. The dorsal margin is extended anteriorly into a median rounded lobe.

The fins are wider (FWI 62.1-*69.5*-73.2) than their lengths (FLI 52.0-*59.0*-64.0). They are attached anteriorly at about the midpoint of the mantle length. The anterior margin of each fin forms a rounded lobe. The lateral angles (72°) of the fins are rounded. The posterior margins are straight and are fused to the mantle separately, except for a point (difficult to see) near the tip of the mantle where they join.

The funnel is large, triangular, and has a broad base. The funnel-mantle locking cartilage is straight, the ends are rounded but the anterior end is slightly narrower; the median groove is shallow. The funnel organ of the holotype is large (9 mm long). The dorsal pad has an inverted V-shape with a slender papilla anteriorly and with prominent ridges on the limbs; each limb is about 2.5 mm wide. The ventral pads are oval and elongated (7 mm long, 3 mm wide).

The head is nearly square in cross section and narrower than the mantle (HWI 21.8-*26.0*-29.3). The funnel groove has a distinct edge on each side. The edges continue posteriorly to form the first pair of nuchal folds which bears the small olfactory papillae. The second and third nuchal folds are crescentlike membranes on each side

---

[2] D = dorsal; V = ventral.

TABLE 1.—Measurements (in millimeters) and counts of *Enoploteuthis obliqua*. TC = RV *Townsend Cromwell*; + = a missing mantle or arm tip, or lost suckers.

Cruise:	TC-48	TC-48	TC-46	TC-44	TC-46	TC-44	TC-44	TC-44
Station:	19	11	9		9	24	24	18
Sex:	Male	(Holotype) Male	Female	Female[1]	Male	Male	?	?
Mantle length	58	55	50	50	41	37+	20	17
Mantle width	19	16	17	16	14	13	9	9
Head width	17	12	14	12	11	8	5.5	7
Fin length	34	32	31	32	21	17	7	8
Fin width	36	38	36	35	30	22	10	12
Arm length								
Right I	29	25+	25	26	20	17+	9	10
Right II	31+	24	26	27	21	17+	12	11
Right III	28+	26	24	30	20	21+	11	9+
Right IV	31	27+	25	31	20	20+	10	9+
Left IV	32	27	25	31	22	22	10	—
Arm hooks/suckers								
Right I	18/24	20/24	23/26	20/22	20/23	10/18	16/—	18/12
Right II	22/20	21/25	24/24	22/20	20/18	20/—	17/—	18/13
Right III	23/—	22/24	24/20	22/16	21/20	20/—	15/—	17/—
Right IV	28/16	30/21	32/15	31/15	30/14	28/—	18/—	26/—
Left IV	28/16	31/16	31/12	31/19	30/18	29/14	17/—	28/—
Tentacles right/left								
Tentacle length	—	47/53	32/—	45/41	29/30	31/—	12/—	14/—
Club length	—	9+/10	8.5/—	13/13	7/—	7/—	3.5/—	3.5/—
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	—	4/4-4/5	4/5-—	4/5-4/5	3/5-4/4	—	—	1/—
Club suckers right/left								
Distal suckers	—	—/13	17/—	14/14	11/—	11/—	—	—
Carpal suckers	—	5/3	5/—	5/5	5/5	4/4	3/4	5/—

[1] From stomach of *Alepisaurus*.

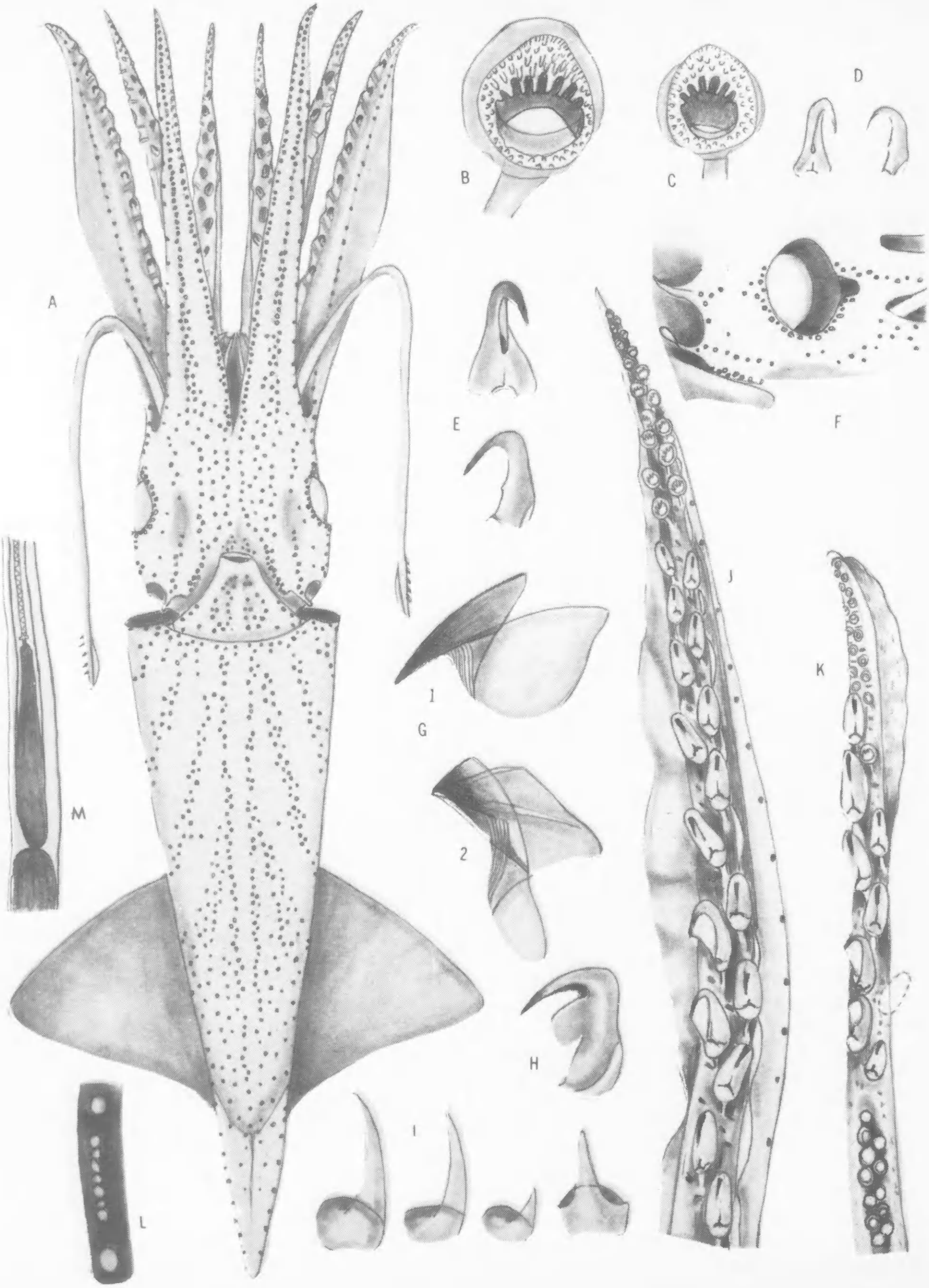
of the neck that are connected to each other posteriorly by a narrow membranous ridge. The third dorsal fold extends dorsally as a membranous ridge, but the ridge does not reach the midline of the head. Dorsal and ventral ocular "windows" are present and the latter easily allows a count of the nine eye photophores on the ventral side of the eyeball. The eye opening is a large, wide, transverse oval with a deep sinus (Fig. 1 F).

The buccal membrane completely hides the buccal mass and surrounding lips. Eight slender supports are joined by slender connectives to the arms in the order DDVD (i.e., all are attached to the dorsal side of the arms except the third pair which are attached to the ventral side of arm III). The inner surface of the buccal membrane is rugose, but without papillae; the lappets are delicate and pointed. The membrane is purple and does not appear much darker than most parts of the body. The chromatophores are small and are scattered evenly on both the supports and the membrane.

The arms are subequal, slender, and much shorter than the mantle length (ALI: I, 48.8-*50.2*-52.0; II, 43.6-*50.2*-54.0; III, 47.3-*51.0*-60.0; IV, 48.8-*53.2*-62.0). They taper gradually to slender tips. The swimming keels are low and poorly developed on the dorsal arms, and they are mainly confined to the distal third of these arms. The swimming keel of arm III is wider than the arm at its greatest width. The lateral membrane or tentacular sheath along arm IV is narrow; it is about half of the arm width proximally and it extends to the tip of the arm. Protective membranes are developed on the ventral side of all arms, but decrease in size in the following order: III, II, I, IV. The dorsal protective membranes on all the arms are low; on arm IV the trabeculae are not evident.

The right ventral arm of the male is hectocotylized. The protective membrane on the medial side of this arm (Fig. 1J) is expanded into an undulating membrane that extends from the eighth pair of hooks to the tip of the arm. The dorsal protective membrane is slightly developed. In the males small tubercles or conical papillae are present between the bases of the hooks and bases of all arms.

All the arms bear two rows of alternating strong hooks, each (Fig. 1E) completely enclosed in a membranous sheath. The distalmost hook is about half the length of the largest one. In both sexes, arm IV has the most hooks. The distal part of each arm is occupied by two rows of suckers with wide apertures and slender stalks. The inner sucker ring bears seven or eight prominent truncated teeth on the distal margin but the proximal margin is smooth (Fig. 1B). The outer ring has numerous pegs (Nixon and Dilly 1977).


A
B
C
D
E
F
G
1
2
H
I
J
K
L
M

The suckers decrease in diameter distally, become globular in shape, and have only three or four blunt teeth.

The tentacles are shorter than the mantle (TLI 62.1-*79.2*-96.4), very delicate and slender. The stalk is laterally compressed, about a third of the width of arm III. The club is not expanded (Fig. 1K). The carpus bears a series of four or five suckers and four, five, or seven pads, and the whole cluster is bordered by a very low ridge on each side. The manus includes a dorsal row of three or four sheathed hooks and a ventral row of four or five slightly larger similarly sheathed hooks (Fig. 1D). These two rows are very close to each other. Marginal suckers are absent. A medial sucker or two may be present in series with the hooks distally. The largest club hook is smaller than any of the arm hooks. The dactylus of the club is occupied by 11 to 17 suckers that are also arranged in two rows. They have long stalks and wide openings. The distal margin of the inner sucker ring bears six or seven slender blunt teeth and the outer sucker ring has numerous pegs (Fig. 1C). Protective membranes are absent. The aboral keel or dorsal membrane is narrow and, at most, about half the length of the club. The tip of the club is rounded and bears a short hoodlike membrane that conceals one or two of the suckers there.

There are two types of light organs on the integument: Large dark ones with pearly white centers and small white ones with very narrow outer pigmented rings. These photophores range in size from small (0.2 mm) to large (0.4 mm), and they are randomly interspersed with each other. The most distinctive feature of this species is the unique arrangement of the mantle photophores. Some of the rows are slanting or oblique (Fig. 1A), instead of the usual straight longitudinal rows described in most other *Enoploteuthis* species. Two median longitudinal rows (two to three photophores in width), separated by an intervening space lacking photophores, extend from the anterior edge of the mantle to the posterior tail. Photophores on the posterior part of the mantle are scattered, those on the anterolateral part are arranged in four oblique rows on each side of the median longitudinal rows. Except for the most posterior row, the oblique rows radiate from the anterior edge of the mantle. The edge of the mantle is lined by a transverse row in which the photophores are closer to each other ventrally than dorsally. A few isolated photophores are present on the dorsal surface of the mantle, none are present on the surface of the fins. The tail has a single row on each side; a few photophores occur on the ventral side, but none are present on the dorsal side.

FIGURE 1.—*Enoploteuthis obliqua* (A-F, K, and L from female paratype, ML (mantle length) 50 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm sucker; C, Tentacular sucker; D, Tentacular hook, oral and lateral aspects; E, Dorsal arm hook, oral and lateral aspects; F, Eye and surrounding area; G, Mandibles: upper (1), lower (2), male, ML 37 mm; H, Dorsal arm sucker, ex-*Alepisaurus* female, ML 50 mm; I, Radular teeth, male, ML 37 mm; J, Hectocotylus, male, ML 41 mm; K, Tentacular club; L, Eye light organs; M, Section of spermatophore, male holotype, ML 55 mm.

Six groups of photophores occur on the funnel: Two broad rows separated by a narrow midline space on the ventral side; a short row of six or seven light organs on each lateral margin (one or two photophores are present in the space between these rows posteriorly); and a group of photophores on each side of the bridles on the dorsal side of the funnel.

There are two patches of light organs, separated by a narrow space, in the apical region of the funnel groove. Six rows are recognizable on the ventral surface of the head, three rows on each side of a narrow midline space devoid of photophores. A row (two or three closely set photophores in width) along the lateral edge of the funnel groove extends anteriorly with increased numbers of photophores medial to each eye. It then bifurcates into two branches: one branch extends along the ventral aboral border of arm IV to a point opposite the last arm hook, the other branch continues distally along the base of the tentacular sheath to the tip of arm IV. The next lateral row of the head photophores extends from near the first nuchal fold anteriorly, although a short gap occurs opposite the lens of the eye at the ventral window, along the head and onto the edge of the tentacular sheath where it continues to near the tip of arm IV. The lateralmost row of the head extends from between the second nuchal fold to the posterior margin of the eye; it continues as a single row of closely set photophores along the edge of the eyelid ventrally to the ventral edge of the optic sinus (Fig. 1F). The dorsal edge of the eyelid is devoid of light organs. From the dorsal edge of the optic sinus the row proceeds along the base of the swimming keel of arm II almost to the tip of the arm. Some small white photophores occur near the eye region between the median and lateralmost rows.

Nine light organs occur in a single row on the ventral side of the eyeball (Fig. 1L). The terminal photophores are larger and are separated by a wide space from a row of seven much smaller ones that lie adjacent to one another.

The teeth of the radula are long and slender (Fig. 1I); the rachidian has distinct cusps on each side. The first lateral teeth are the shortest.

The mandibles of a young male (ML 40 mm) have distinct growth lines on the wings. The rostrum is heavily pigmented; the edges are sharp and the tip of the upper mandible is very pointed (Fig. $1G_1$). The gular plate of the lower mandible is strengthened by three stout ribs (Fig. $1G_2$).

The gladius has a strong rachis which is rounded anteriorly and thickened medially. The thin vanes are widest at about the midpoint of the total length. The rounded posterior cone is shallow and thin.

A single spermatophore was found in the spermatophoric sac of the holotype (ML 55 mm), and its measurements are given below:

Spermatophore segment	*Length (mm)*
Entire spermatophore	11.5
Spiral filament	4.5
Cement body	1.5
Sperm reservoir	5.5

The spiral filament is slightly sculptured at the aboral end by some irregular ridges. The cement body has a small collar at the oral end (Fig. 1M). A few spiral turns are visible behind the spermatophore cap.

Young individuals: Small specimens (ML 6.0-20.0 mm) are easily separated from other species of *Enoploteuthis* by the unique oblique rows of photophores on the mantle. Early development of the oblique rows are shown in Figure 2Aa and b in specimens ML 7 and 9 mm, respectively. Arm hooks are formed early; six to nine hooks are already present in the arms at ML 6.0 mm. But tentacular hooks appear much later; a ML 17 mm specimen has one tentacular hook and another (ML 20 mm) has none at all. Only two rows of suckers are present on the club.

Remarks: A female specimen tentatively assigned to this species (from the stomach contents of an *Alepisaurus*) exhibits certain features not observed in other specimens of the same or nearly the same size. The arm and tentacular hooks have flattened processes (Fig. 1H). Furthermore, this specimen shows a slight variation in the arrangement of photophores: some photophores occur on the median space of the mantle.

The closest species to *E. obliqua* is *E. leptura* (Leach 1817) from the Atlantic. Both *obliqua* and *leptura* have slender tentacles and clubs. There are few suckers (<20) arranged in two rows on their clubs. However, *obliqua* has fewer tentacular hooks (at most 9) while *leptura* has more (6-12). The carpal cluster is elongate and without prominent ridges in both species. Their spermatophores show similar characteristics: very little sculpture in the spiral filament and one small collar on the cement body.

The specific name *obliqua* reflects the arrangement of the mantle photophores. The oblique arrangement of light organs on the mantle was described earlier by Okutani (1974). His three immature specimens (ML 23.8-25.8 mm) from the EASTROPAC collection and a fourth specimen from the invertebrate collection of the Scripps Institution of Oceanography are all referable to *E. obliqua*. His material was collected in the eastern Pacific.

Distribution: Equatorial regions of the central and eastern Pacific.

Enoploteuthis octolineata n. sp.

(Figs. 3, 2C; Table 2)

Holotype: Female, ML 71 mm, HMS-47, Stn. 58, 02°56′N, 150°03′W, 4 November 1958, 212 m, USNM 577607.

Paratypes: 1 female, ML 75 mm, TC-43, Stn. 52, 00°01′N, 145°03′W, 28 May 1969, 50 m, USNM 729721. 1 female, ML 56 mm, TC-46, Stn. 37, 03°23′N, 145°04′W, 26 October 1969, 50 m, USNM 729720. 1 male, ML 46 mm, TC-48, Stn. 50, 03°29′N, 144°58′W, 17-18 April 1970, 50 m, USNM 729708.

Other material: 1 specimen, ML 10 mm, HMS-47, Stn. 51, 00°44′S, 149°46′W, 2 November 1958, 576 m. 1 specimen, ML 25 mm, HMS-47, Stn. 58, 02°56′N, 150°03′W, 4 November 1958, 212 m. 1 specimen, ML 15 mm, CHG-89, Stn. 5, 02°40′N, 157°31′W, 28 July 1966, 120-240 m. 1 specimen, ML 15 mm, TC-43, Stn. 12, 12°11′N,

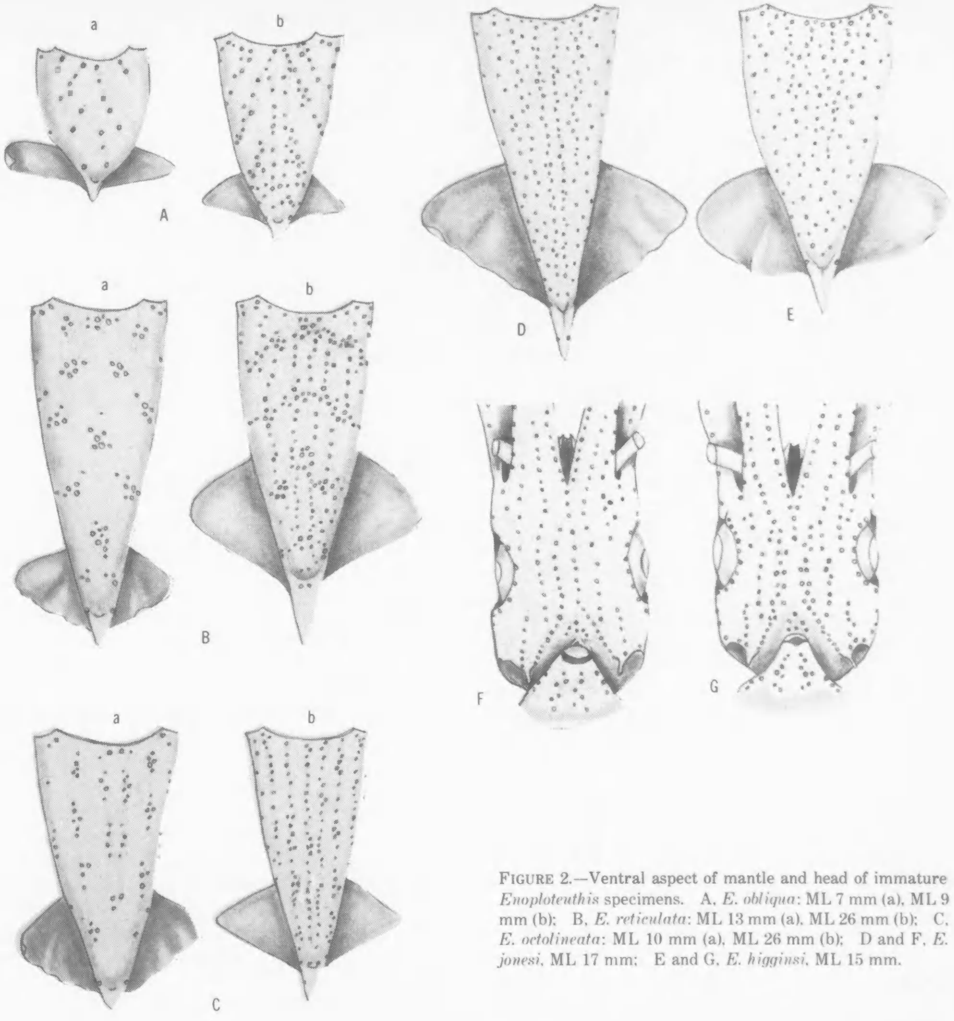


FIGURE 2.—Ventral aspect of mantle and head of immature *Enoploteuthis* specimens. A, *E. obliqua*: ML 7 mm (a), ML 9 mm (b); B, *E. reticulata*: ML 13 mm (a), ML 26 mm (b); C, *E. octolineata*: ML 10 mm (a), ML 26 mm (b); D and F, *E. jonesi*, ML 17 mm; E and G, *E. higginsi*, ML 15 mm.

145°11′W, 9 May 1969, 20 m. 1 specimen, ML 20 mm, TC-43, Stn. 26, 07°33′N, 144°50′W, 15 May 1969, 50 m. 3 specimens, ML 19-30 mm, TC-43, Stn. 38, 03°30′N, 145°06′W, 20 May 1969, 50 m. 2 specimens, ML 21 and 40 mm, TC-43, Stn. 42, 03°32′N, 144°59′W, 22 May 1969, 50 m. 1 specimen, ML 24 mm, TC-43, Stn. 48, 00°04′N, 145°07′W, 26 May 1969, 50 m. 2 specimens, ML 20 and 22 mm, TC-43, Stn. 52, 00°01′N, 145°03′W, 28 May 1969, 50 m. 1 specimen, ML 26 mm, TC-44, Stn. 26, 07°14.8′N, 144°58.8′W, 14 July 1969, 20 m. 1 specimen (from *Alepisaurus* stomach contents), ML 28 mm, TC-44, Stn. 44, 03°49.9′N, 145°18′W, 22 July 1969, 50 m. 1 specimen, ML 20 mm, TC-44, Stn. 56, 00°15.2′N, 144°43.9′W, 29 July 1969, 50 m. 1 specimen, ML 25 mm, TC-44, Stn. 68, 03°39′S, 144°54.5′W, 3 August 1969, 75 m. 1 specimen, ML 36 mm, TC-46, Stn. 41, 03°19′N, 145°03′W, 28 October 1969, 50 m. 2 specimens, ML 14 mm, TC-46,

TABLE 2.—Measurements (in millimeters) and counts of *Enoploteuthis octolineata*. HMS = RV *Hugh M. Smith*; TC = RV *Townsend Cromwell*; + = missing arm tips and lost suckers.

Cruise:	HMS-47	TC-43	TC-46	TC-48	TC-48	TC-44	HMS-47	TC-43
Station:	58	52	37	50	92	26	58	12
Sex:	(Holotype) Female	Female	Female	Male	?	?	?	?
Mantle length	71	75	56	46	33	26	25	15
Mantle width	26	27	21	18	13	11	13	6
Head width	24	21	16	14	10	10	12	5
Fin length	50	52	38	30	19	15	15	7
Fin width	54	56	42	32	23	20	20	8
Arm length								
Right I	43	49	28+	32	23	16	15	8
Right II	42	46	32	[1]32	24	16	18	8
Right III	42	50	31	38	25	18	17	7
Right IV	42	52	38	33	25	16	16	9
Left IV	45	54	35	31	25	18	16	—
Arm hooks/suckers								
Right I	21/36	23/26	20/23+	20/—	—	21/25	16/14	16/12
Right II	22/32	22/24	21/21	18/—	22/—	22/22	21/—	16/14
Right III	25/27	24/28	22/22	21/18	20/—	21/24	23/—	15/11
Right IV	29/25	34/38	32/25	29/23	28/10+	30/22	21/—	18/10
Left IV	30/30	32/34	31/26	29/20+	26/12	29/27	29/12	—
Tentacles right/left								
Tentacle length	75/80	70/70	53/—	43/44	39/37	15/16	25/—	13/—
Club length	19/18	—	14/15	12/13	10/9	5/5	5/—	4/—
Club hooks								
(Right (dorsal/ventral)-left (dorsal/ventral)	4/5-4/6	—-6/5	4/6-4/6	5/5-4/6	4/5-—	4/5-4/6	5/5-—	—
Club suckers right/left								
Distal suckers	16/17	—	14/14	14/16	10/—	—/19	—	—
Carpal suckers	3/5	6/4	6/5	5/6	4/—	6/4	3/—	—

[1] Length of left arm.

Stn. 45, 03°29′N, 144°54′W, 30 October 1969, 50 m. 1 female, ML 56 mm, TC-46, Stn. 47, 03°23′ N, 145°04′W, 31 October 1969, 115 m. 2 specimens, ML 16 and 20 mm, TC-47, Stn. 45, 03°28′ N, 144°59′W, 3-4 February 1970, 50 m. 1 specimen, ML 39 mm, TC-48, Stn. 35, 07°18′N, 144° 47′W, 11-12 April 1970, 50 m. 1 female, ML 49 mm, TC-48, Stn. 50, 03°29′N, 144°58′W, 17-18 April 1970, 50 m. 1 specimen, ML 33 mm, TC-48, Stn. 92, 00°08′N, 145°00′W, 28 April 1970, 50 m.

Description: The mantle (MWI 36.0-*37.3*-39.1) is cylindrical and tapers gradually toward the end of the blunt tail. Ventrally the anterior edge of the mantle is only slightly excavated and the lateral angles are pointed and low. The anterior dorsal lobe is rounded and also low.

The fin lengths are more than half of the mantle length (FLI 65.2-*68.0*-70.4) and the combined width of both fins is less than the mantle length (FWI 69.6-*73.9*-76.1). The anterior margins project into rounded lobes near their anterior attachments. The lateral angle (about 70°) is rounded and the posterior margin is slightly convex.

The funnel is large; its length equals its width. The funnel-mantle locking cartilage is simple; its anterior end is slightly narrower and more pointed than the rounder posterior end. The funnel valve is a wide semilunar flap; its anterior edge reaches the edge of the funnel opening.

The head (HWI 28.0-*30.2*-33.8) is narrower than the mantle, almost square in cross section, slightly rounded on the top, and is deeply excavated on its posteroventral surface to form a large funnel groove. The dorsal and ventral ocular "windows" are distinct. The eye opening has a deep sinus (Fig. 3G). Three nuchal folds lie on each side of the head; the closest fold to the funnel bears at its posterior end the tonguelike olfactory papilla. These nuchal folds are united to each other by a narrow posterior membrane, although this membrane does not reach the dorsal midline.

The buccal membrane is purple and the eight supports are joined by connectives to the arms in the order DDVD. The membrane is pigmented more heavily than the supports. The lappets are delicately pointed, and the inner surface of the buccal funnel is very rugose but lacks papillae.

The arms are subequal and shorter than the mantle (ALI: I, 60.6-*65.2*-69.7; II, 57.1-*61.8*-69.6; III, 55.4-*66.0*-82.6; IV, 59.2-*66.7*-72.0). They are nearly square at their bases and taper into fine points. Arms I and II have very low keels; arm I is keeled to about half its length and arm II to

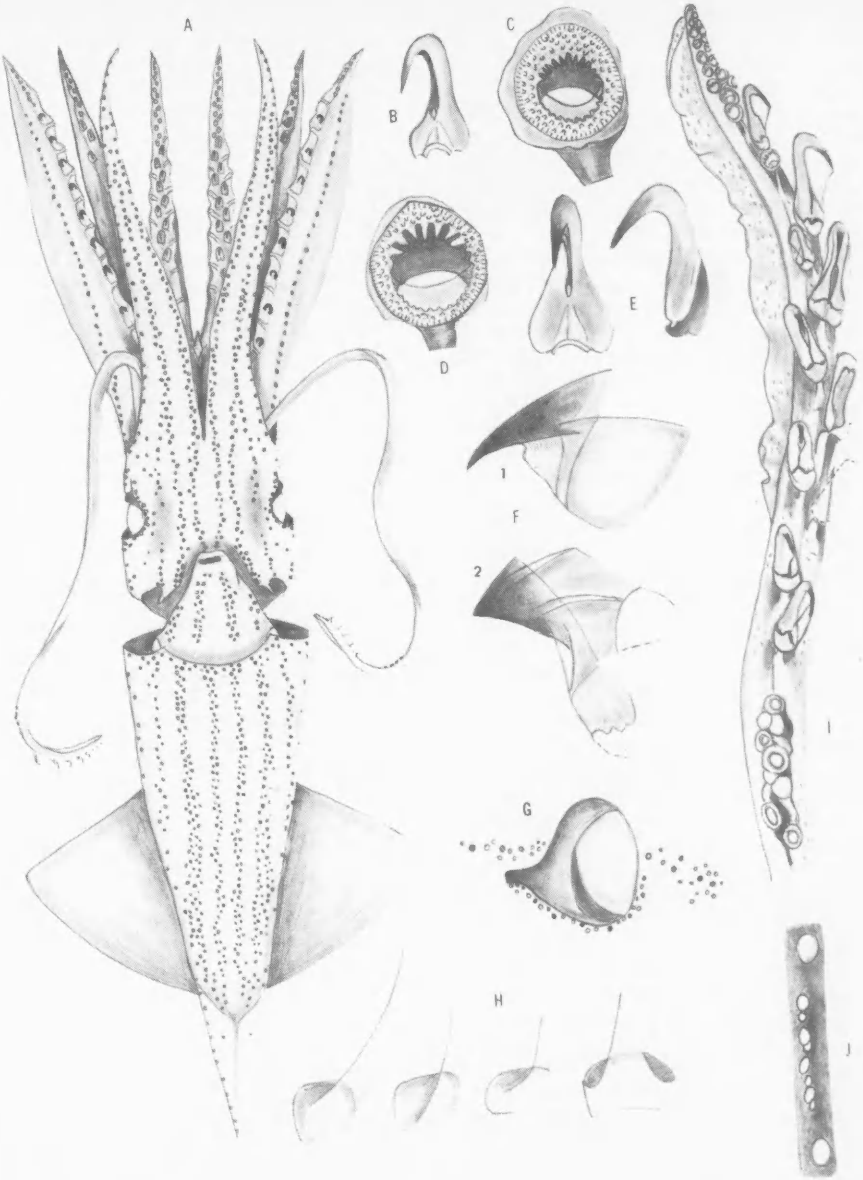


FIGURE 3.—*Enoploteuthis octolineata.* (A-E, G, I, and J from female paratype, ML (mantle length) 75 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Tentacular hook; C, Tentacular sucker; D, Dorsal arm sucker; E, Dorsal arm hook, oral and lateral aspects; F, Mandibles: upper (1), lower (2), male, ML 25 mm; G, Eye and surrounding area; H, Radular teeth, ML 25 mm; I, Tentacular club; J, Eye light organs.

about one-third. The swimming keel of arm III is about as wide as the arm. The tentacular sheath is narrow, about half the width of arm IV near the base. The dorsal and ventral protective membranes are developed on all the arms and extend to the arm tips. The ventral membranes are wider on arm III, although they do not reach the top of the hooks. The protective membranes of arm IV are very narrow, except those on the hectocotylus of the male.

The ventral protective membrane of right arm IV (hectocotylus) of the immature male paratype (ML 46 mm) is slightly enlarged into a narrow undulating membrane, about 1 mm wide, opposite the eighth and ninth pairs of hooks. The dorsal protective membrane is very narrow.

The arm hooks (Fig. 3E) are biserial and are completely covered by sheaths. Arm IV is slightly longer than the other arms, and has the greatest number of hooks. The suckers on the distal part of the arms can be separated into two types. The distalmost suckers are markedly reduced in size, are globular in shape with small apertures, and lack teeth. The proximal suckers have long stalks and wide openings. The inner rings of these suckers have eight to nine large pointed teeth distally, very irregular, smaller teeth proximally, and a wide shelf at the bottom half. The outer ring bears numerous pegs (Fig. 3D).

The tentacles are weakly developed, about as long as the mantle (TLI 93.3-*98.4*-112.7) and very narrow (only about one-third of the width of arm III). The cross section is almost triangular. The club is also narrow (Fig. 3I). The aboral keel extends from opposite the second hook to the tip of the club. Protective membranes are absent, but a short hoodlike membrane is present at the blunt tip. The carpal cluster is composed of a series of three to six smooth-ringed suckers and three to five rounded pads which are biserially arranged in an elongate patch. One of the paratypes (ML 75 mm) has two additional suckers on the stalk located a short distance from the right carpal cluster (such suckers not present in other specimens); corresponding pads, if any, were not seen on the opposite tentacle due to damage. The manus has a total of 9 to 11 sheathed hooks and an occasional sucker in the distal part. These alternating dorsal and ventral hooks are only slightly separated medially. Hooks on the dorsal row are smaller. The hooks (Fig. 3B) resemble the arm hooks in structure, except for the relatively narrower bases of club hooks and their relatively smaller size. The few (16 or 17) distal suckers on the dactylus are also biserial. They have long stalks and wide openings; the inner rings have about 10 sharp teeth distally, a series of smaller denticulations proximally, and an inner shelf at the proximal bottom part (Fig. 3C). The outer ring bears pegs.

There are two types of skin photophores: Very dark ones with whitish centers and white ones with very thin outer black rings (in preservation). The smallest is about half the size of the largest, but intermediate sizes occur. Both types appear randomly interspersed. On the ventral side of the mantle there are eight distinct rows separated by spaces wider than the rows themselves. A continuous midline space is present from the anterior of the mantle to the tail (Fig. 3A). Four parallel rows of varying widths lie on either side of this space. The first and second lateral rows extend from the excavated part of the mantle to the tail. The third row extends from opposite the lateral angle of the mantle to the tip of the mantle, occurring along the lateral margins of the tail as a single row of evenly spaced photophores. The photophores of these rows tend to disperse at the posterior end, particularly the second row, and the rows become slightly intermingled, but each row remains recognizable. The fourth or lateralmost row is composed of widely spaced light organs forming a single line that becomes somewhat irregular opposite the region of the fins. Small photophores are dispersed on the dorsal side of the mantle, but there are none on the fins or on most of the tail except for the lateral row mentioned above and a few very small ones ventrally. A transverse row that has fewer and more widely separated photophores dorsally runs along the edge of the mantle.

Four narrow rows of photophores separated by wide spaces are present on the ventral half of the funnel. There are two additional rows on the dorsal side, one on each side of the bridles.

There are eight separate rows of photophores on the ventral half of the head, four rows on each side of a wide median space. The first row lateral to the midline space originates anterior to the bridle within the apex of the funnel groove and continues directly to the ventral aboral side of arm IV and ends just beyond the distalmost arm hook. The second lateral row begins at the posterior end of the funnel groove and runs along the edge of the groove, over the ventral part of the head, and proceeds anteriorly along the base of the tentacular sheath to the tip of arm IV. The third row extends anteriorly from the base of the first nuchal fold but is interrupted by the window of the eye, and subsequently divides. One branch unites with the second row at a short distance from the base of the ventral arm. The other branch continues laterally along the edge of the tentacular sheath to the tip of arm IV. The fourth row begins opposite the second nuchal fold and proceeds to the posterior margin of the eye opening and runs along the edge of the eyelid ventrally to the optic sinus (Fig. 3G). The dorsal half of the eyelid has no light organs. From the upper edge of the optic sinus the fourth row continues along the base of the swimming keel of arm III to almost opposite the last arm hook. An additional short arc-shaped row of very small white photophores, set far apart, lies between the third and fourth rows on the posteroventral eye region. This short row is inconspicuous and can easily escape detection.

The light organs on the eyeball vary from 9 to 10. The large terminal photophores are separated by a space from a series of eight or seven adjacent round to oval smaller light organs (Fig. 3J) of varying dimensions.

The radula has seven long, slender, slightly curved teeth in each transverse row. The rachidian tooth has pointed cusps, one on each side. The lateralmost teeth are longest (Fig. 3H).

The mandibles are strong and heavily pigmented. The rostrum of the upper mandible is very pointed and the edges are sharp (Fig. $3F_1$). The lower mandible has three distinct ridges (Fig. $3F_2$). In a specimen ML 25 mm the wings of both halves are transparent.

The gladius is featherlike and the rachis is thickened into a rounded ridge dorsally. The vanes are fragile and narrow. The cone is thin and narrow, but rounded posteriorly. The thickened edge of the vanes described by Roper (1966, fig. 14) in *E. anapsis* is only slightly indicated here.

There are no spermatophores in the largest male paratype (ML 46 mm). The hectocotylus is not fully developed; the lappet is only 1 mm wide and there are no tubercles on the inner surface of the arms. Numerous sperm reservoirs are present in one of the females (ML 75 mm). These are about 6 mm long and are attached in two areas: on the inner wall of the mantle (opposite the midpart of each funnel retractor muscle) and in the concave inner wall of the retractor muscles themselves. The same female is gravid; the diameter of an egg taken from the ovary is slightly <1 mm.

Young individuals: Immature specimens (ML 10-30 mm) have six to eight rows of light organs on the mantle. These rows first appear as a series of elongate patches of large photophores separated by spaces which later develop smaller photophores (Figs. 2Ca, b). At ML 10 mm, all the arms have hooks. The club has two rows of suckers and no hooks. Five of the suckers are set apart proximally and presumably become carpal suckers. At ML 15 mm there are three hooks on the club; by ML 20 mm the club has eight hooks. The tentacles of these immature individuals are shorter than the mantle (TLI 50.0-*68.4*-86.7). The light organs of the eye do not develop simultaneously: some of the smaller individuals have only seven or eight (the two terminal photophores and five or six inner ones).

Remarks: The most distinctive feature of this species is the eight well-defined rows of photophores, separated by wide spaces, on the mantle. In some respects this species resembles *E. leptura* in the shape of the fins and the structure of the clubs and tentacles. However, the latter species has only seven rows of photophores on the mantle, one of which arises from either of the most median pair of rows and does not reach the mantle. This feature is also found in juveniles. The arrangement of the photophores on the head also differs. The third lateral row is unbranched in *E. leptura*.

Distribution: Central Pacific, equatorial waters. Based on sampling for the present collection, *E. octolineata* does not seem to occur in the Hawaiian area.

Enoploteuthis jonesi n. sp.
(Figs. 4, 2D, F; Table 3)

Holotype: Male, ML 47 mm, TC-7, Stn. 12, off Milolii, Hawaii, 16 August 1964, 9-13 m, USNM 729717.

Paratypes: 1 male, ML 35 mm, CHG-89, Stn. 24, 14°55.1′S, 164°02′W, 10 February 1966, 90-130 m, USNM 729699. 1 female, ML 82 mm, TC-7, Stn. 12, off Milolii, Hawaii, 16 August 1964, 9-13 m, USNM 577608. 1 female, ML 40 mm, TC-32, Stn. 28, 20°58.6′N, 158°33.7′W, 25 July 1967, 92-122 m, USNM 729707.

Other material: 1 male, ML 27 mm, CHG-89, Stn. 14, 06°06.9′S, 157°44.2′W, 3 February 1966, 70-80 m. 1 specimen, ML 22 mm, CHG-89, Stn. 29, 04°05′S, 167°51′W, 14 February 1966, 120-135 m. 1 specimen, ML 17 mm, CHG-89, Stn. 31, 01°01′S, 168°06′W, 15 February 1966, 90-150 m. 1 specimen, ML 11 mm, TC-32, Stn. 37, 20°59.1′N, 158°12.7′W, 15 August 1967, 55-123 m. 1 female, ML 30 mm, TC-32, Stn. 39, 20°59.6′N, 158°29.3′W, 15 August 1967, 63-101 m. 1 female, ML 35 mm, TC-32, Stn. 46, 20°57.6′N, 158°28.7′W, 18 August 1967, 77-118 m.

Description: The mantle is long, cylindrical, and narrow (MWI 24.4-*34.3*-40.7). The width at the edge is only slightly greater than that at the middle and the sides taper into a blunt tail. The mantle is muscular except for the tail which is thin-walled and translucent, yet very firm. The ventral anterior excavation of the mantle is shallow and the lateral angles and middorsal projection are low and blunt.

Each fin is triangular and their combined width is about three-fifths to four-fifths of the mantle length (FWI 65.9-*74.0*-80.0). The fins are shorter than their combined width (FLI 62.9-*67.5*-70.0). The anterior margin is rounded and the posterior margin is slightly concave. The lateral angles are sharp, about 75°.

The funnel is triangular with a broad base. The funnel-mantle locking cartilage is simple and typical of the genus. The groove is shallow and it spreads out toward the more rounded posterior end of the cartilage. The funnel organ is large; the dorsal pad has a papilla and well-developed ridges; the ventral pads are oval with pointed anterior ends. The semilunar funnel valve is wide and its anteriormost edge does not reach the edge of the funnel opening.

The head is nearly square in cross section, as long as it is wide, and nearly as broad as the mantle (HWI 25.6-*30.9*-37.5). Both dorsal and ventral ocular "windows" are distinct. The eye opening is a wide oval (triangular when constricted) and has a moderately deep sinus. The three crescentic nuchal folds are prominent. The olfactory papilla is tonguelike and arises from the nuchal fold nearest to the funnel. The funnel groove is moderately deep and the sides of this excavation are steep.

The buccal funnel has eight stout supports connected to the arms in the order DDVD. The lappets are pointed; the inner wall of the buccal membrane is very rugose and carries papillae. Both membrane and supports are covered with small fine chromatophores, but the membrane appears darker.

The arms are of moderate length (ALI: I, 40.0-*45.4*-50.0; II, 43.9-*48.8*-51.9; III, 47.6-*51.3*-59.2;

TABLE 3.—Measurements (in millimeters) and counts of *Enoploteuthis jonesi*. TC = RV *Townsend Cromwell*; CHG = RV *Charles H. Gilbert*; + = lost suckers.

Cruise:	TC-7	TC-7	TC-32	CHG-89	TC-32	CHG-89	CHG-89	CHG-89
Station:	12	12	28	24	39	14	29	31
		(Holotype)						
Sex:	Female	Male	Female	Male	Female	Male	?	?
Mantle length	82	47	40	35	30	27	22	17
Mantle width	20	14	15	13	11	11	10	9
Head width	21	13	15	11	9	9	8	6.5
Fin length	56	32	28	23	21	17	14	10.5
Fin width	54	34	32	25	24	20	18	14
Arm length								
Right I	35	23	16	15	15	13	[1]9	8
Right II	36	24	19	17	15	14	11.5	9
Right III	39	23	20	17	16	16	12	10
Right IV	46	28	22	20	15	15	13	11
Left IV	46	28	21	19	15	15	—	—
Arm hooks/suckers								
Right I	26/41	20/48	21/—	19/30	17/22	14/18	[1]15/16	11/19
Right II	27/32	23/38	22/—	16/20	18/18	18/18	17/18	14/14
Right III	28/36	21/28	22/—	22/22	17/15	20/18	18/16	14/21
Right IV	31/15	21/10	23/—	25/9	21/15	21/21	19/—	22/20
Left IV	31/22	28/38	25/—	26/16	21/18	21/12+	19/—	—
Tentacles right/left								
Tentacle length	—/86	61/—	65/68	43/—	51/46	48/51	42/42	23/27
Club length	—/20	15/—	15/15	12/—	11/11	11/11	9/9	7/7
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	—-7/7	7/7-—	6/7-6/7	7/6-—	7/7-6/7	—-7/6	7/7-—	6/6-5/7
Club suckers right/left								
Distal suckers	—/68	64/—	72/52+	70	64/72	—/64	72/—	68/64
Carpal suckers	—/4	4/—	3/4	4/—	3/4	—/4	3/—	4/4

[1] Length or count of left arm.

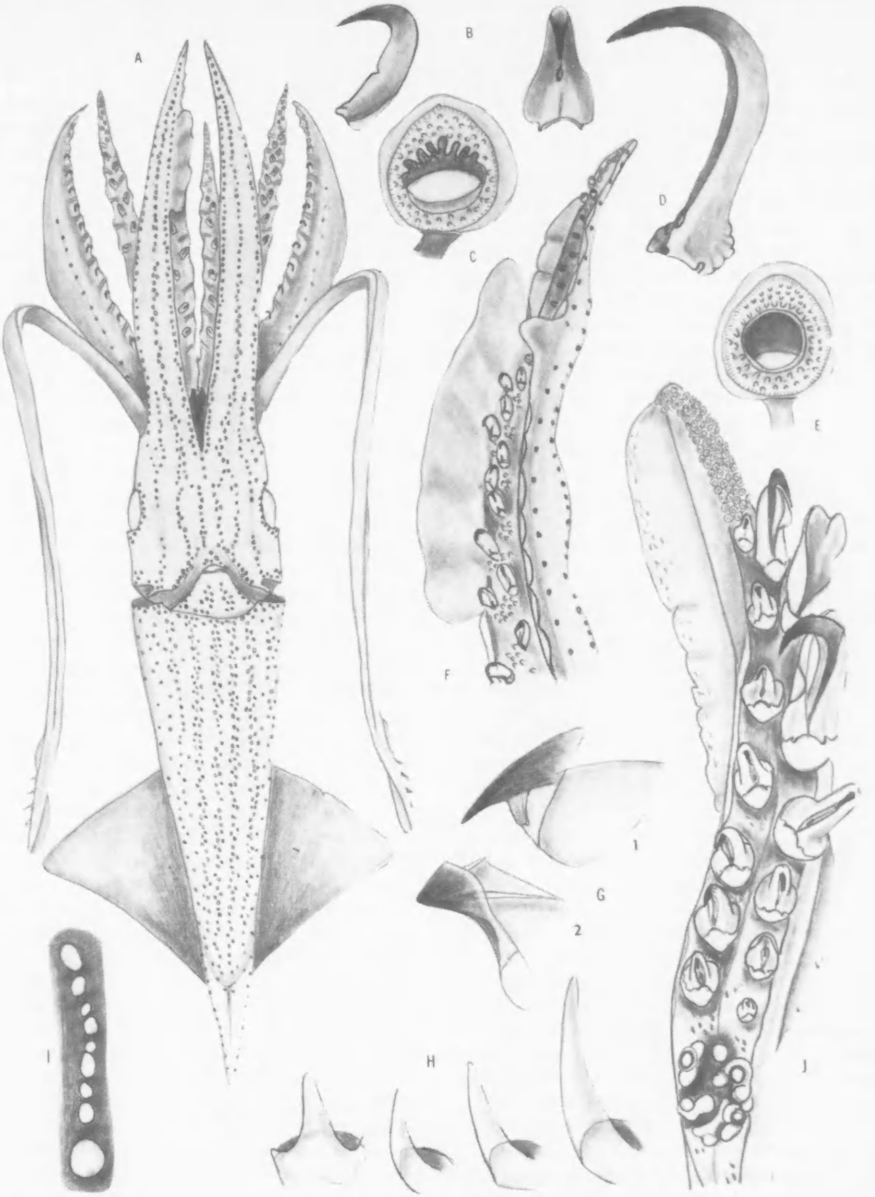


FIGURE 4.—*Enoploteuthis jonesi.* (A-F, I, and J from male holotype, ML (mantle length) 47 m; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm hook, oral and lateral aspects; C, Dorsal arm sucker; D, Tentacular hook; E, Tentacular sucker; F, Hectocotylus; G, Mandibles: upper (1), lower (2), ML 27 mm; H, Radular teeth, ML 27 mm; I, Eye light organs; J, Tentacular club.

IV, 50.0-*55.0*-59.6). Arm IV is longest in both sexes. The arms are nearly square in cross section and they taper distally into fine delicate tips. The keels of arms I and II are confined mainly to the distal halves of the arms. The swimming keel of arm III is as wide as the arm at its midpoint. The lateral membrane (or tentacular sheath) of arm IV is moderately wide and extends to the tip of the arm. Dorsal and ventral protective membranes are present in all the arms. The ventral membrane is more developed than the dorsal, particularly on arm III.

In the males the right arm IV is hectocotylized. The ventral protective membrane on this arm forms a very wide lappet that extends from about the middle half, opposite the sixth pair of hooks, to about four-fifths of the arm length. Distally the membrane is much narrower and tapers to the arm tip (Fig. 4F). The dorsal protective membrane is slightly modified: a small tongue-like flap is developed opposite the distal end of the larger medial lappet. In addition, the males have numerous conical tubercles at the bases of the oral surface of all the arms and between the bases of all the hooks.

The biserial and regularly arranged hooks are completely sheathed by membranes (Fig. 4B). The distal arm suckers have long stalks. Each inner ring has eight teeth on its distal half and none on the smooth proximal half (Fig. 4C). The outer rings bear pegs all around. The suckers are progressively smaller distally; the distal suckers assume a globular shape, have small apertures, no teeth, and no outer rings.

The tentacles are longer than the mantle (TLI 104.9-*153.3*-188.9) and are about twice the length of the longest arm. The stalk is oblong in cross section near the base, very muscular, and almost as thick as arm III. The proximal part of the club is as narrow as the stalk or only slightly expanded. The club becomes unusually narrow in the distal one-third (Fig. 4J). The tip is blunt. The aboral keel is about one-half of the club length. A semilunar membrane is present on the ventral or oral side; it extends between the carpal area and the fourth pair of hooks. Protective membranes are developed on the ventral side but are rudimentary dorsally. Protective membranes are absent on the dactylus. The carpal cluster consists of three or four smooth-ringed suckers and several rounded pads in a compact round cluster together with some irregular grooves and ridges. There are 13 or 14 robust hooks in two rows on the club. The ventral row includes a series of greatly enlarged hooks. The hooks (Fig. 4D) are enclosed by membranes but the tips are exposed. These hooks have very broad bases and are set in rounded shallow excavations. Marginal suckers are absent. Twelve to 18 transverse rows of 4 small suckers per row occupy the narrow dactylus. About 12 of these suckers at the tip are slightly larger than the immediately preceding transverse row, thus forming a cluster at the tip of the club. All the club suckers have smooth inner rings (Fig. 4E). The pegs on the outer ring are moderately long and may hide the smooth edge of the inner ring from view.

The integumentary photophores occur in different sizes ranging from about 0.2 to 0.4 mm. A photophore may appear dark or very pale, depending on the extent of pigmentation. Many of the larger photophores are heavily pigmented, except for a small central area. Most of the smaller photophores are pale because pigmentation is confined to the periphery in the form of a very thin dark ring. Intermediate conditions between these extremes occur. At first glance the photophores on the mantle appear scattered at random, but on closer examination one can recognize four multiserial, ill-defined rows: two rows on each side of a very narrow midline space that extends from the anterior opening of the mantle to the tail and bounded laterally by a broad zone of photophores (Fig. 4A). Each row consists of large and small photophores set near each other; smaller and whiter ones occupy the central part of the row, while the larger and more conspicuously darker ones are located mostly on the outer area of the row. These rows become more difficult to distinguish posteriorly. A single row of evenly spaced photophores extends along the lateral margins of the tail. Numerous photophores occupy the ventrolateral surface and some single photophores, generally small ones, are scattered on the dorsal surface of the mantle, except near the midline. The edge of the mantle is lined by a single row of photophores; the photophores are spaced progressively farther apart toward the dorsal midline.

The funnel has six groups of photophores: Two rows separated by a midline space on the ventral side; a short row on each lateral side; and two dorsal rows, one on each side of the bridle.

A small triangular cluster of photophores is situated in the apex of the funnel groove. A space in the ventral midline of the head is broken by a short row of two or three photophores that bifurcates at the fork of the ventral arms; each branch continues along the ventral aboral side of arm IV to almost the tip. A row of closely set photophores runs along the edge of the funnel groove and divides near the apex of the groove into two branches, each with photophores in single file. The branches reunite near the base of arm IV. The row continues distally along the base of the tentacular sheath to the tip of the arm. The third lateral row on the head begins anterior to the first nuchal fold, has a gap at the window of the eye, and then continues and splits into two branches: A medial branch that continues anteriorly and ends near the base of arm IV at the midline of the tentacular sheath and a lateral branch that extends along the edge of the tentacular sheath and terminates about the level of the last hook on arm IV. The lateralmost row on the head also starts at the first nuchal fold, continues along the nuchal crest, and turns toward the posterior eyelid where it runs along the ventral edge to the optic sinus. The row begins again on the dorsal edge of the optic sinus, continues along the base of the swimming keel of arm III, and stops at about three-fifths of the arm length. The dorsal eyelid lacks photophores.

There are nine irregularly spaced photophores on the ventral part of the eyeball (Fig. 4I). The posteriormost light organ is larger than the anteriormost which in turn is larger than the remaining seven light organs. The latter are slightly different from each other in size and shape.

The teeth of the radula are long (lateralmost teeth are longest), blunt, and slightly curved (Fig. 4H). Of the seven teeth only the rachidian tooth has small lateral cusps.

The upper mandible of a small specimen (ML 30 mm) has distinct growth lines on the wings (Fig. 4G_1). The riblike ridges on the gular plate of the lower mandible are well developed (Fig. 4G_2).

The gladius is feather-shaped. The rachis is blunt anteriorly and forms a strong ridge dorsally through its length. The vanes are narrow, widest at about a third of the length of the gladius. The posterior end is curved inward ending in the cone.

The largest female (ML 82 mm) is gravid; the ovaries are distended and extend to the posterior part of the mantle cavity. The eggs are opaque and about 1 mm in diameter.

None of the males have spermatophores.

Young individuals: Immature individuals (ML 11-22 mm) have relatively wider mantles (MWI 45.5-*57.0*-72.7) than adults. At ML 11 mm the arms have the following armature: 1 to 3 suckers proximally, 7 to 12 hooks, and 15 to 20 suckers distally. The tentacles are distinctly longer than the mantle (TLI 172.7). The club has three hooks along with nine biserial suckers on the manus. Two of the suckers are slightly set apart (future carpal suckers). Four rows of minute suckers are located on the dactylus. At ML 17 mm the arms have no proximal suckers, 12 to 18 hooks, and 19 to 21 distal suckers. The club resembles that of the adult, except that two marginal suckers are present on the dorsal distal side of the manus and although there are already four carpal suckers, the carpus is still not completely developed. The photophores on the mantle are not distinctly arranged into rows, except for two medialmost rows which are separated by a narrow space (Fig. 2D). The rows on the head are each composed of photophores in single file (Fig. 2F). The number and position of the rows agree with those of the adult.

Remarks: Adults of this species resemble superficially *E. chuni* Ishikawa 1914 from Japan, but they are easily distinguished by the photophore pattern of the head and arms. *Enoploteuthis chuni* has seven rows of photophores on the head (including the rows passing along the ventral eyelids) (pl. XX, fig. 1, Sasaki 1920), whereas *jonesi* has six rows. There is a distinct midventral multiserial row on the head of *chuni*, whereas the ventral midline of *jonesi* is a clear space, except for two or three single photophores near the fork of the ventral arms anteriorly. Some rows of photophores on the head divide and reunite in *jonesi*, a condition absent in *chuni*. The row of photophores at the base of the swimming keel of arm III reaches the tip of the arm in *chuni*, but in *jonesi*, the same row ends slightly beyond one-half to three-fifths of the arm length. These observations were confirmed by T. Okutani of the Tokai Regional Research Laboratory (presently with the National Science Museum, Tokyo) who kindly examined specimens of *E. chuni* from Suruga Bay and compared them with illustrations of *E. jonesi* sent to him. In addition, there are more distal club suckers in *chuni* (90) than in *jonesi* (64-72) and these suckers are toothed in *chuni* and smooth in *jonesi*.

The counts and measurement of *E. jonesi* overlap those of *E. anapsis* Roper, 1964 from the tropical Atlantic and Caribbean. These species exhibit the following differences: 1) The midline space on the mantle in *jonesi* continues uninterrupted to the tail, but this space in *anapsis* has some scattered photophores near the tail; 2) the row that traverses the window on the ventral side of the head is bifurcate in *jonesi* whereas it is single in *anapsis*. The tentacles and clubs of *anapsis* are relatively longer than those of *jonesi*. The distal club suckers are more numerous in *jonesi* (64-72) than in *anapsis* (40-50).

This species is named after Everet C. Jones, former fishery biologist at the Honolulu Laboratory. It was under the supervision of E. C. Jones that the specimens collected during some of the cruises reached me in good condition.

Distribution: Central Pacific, Hawaiian waters, and equatorial region.

Enoploteuthis higginisi n. sp.
(Figs. 5, 2E, G; Table 4)

Enoploteuthis species B, Young 1978: figure 9B.

Holotype: Male, ML 37 mm, *Teritu*, Stn. 6 off Waianae, Oahu, September 1969, 110 m, USNM 729710.

Paratypes: 1 male, ML 35 mm, CHG-89, Stn. 11, 06°04.9′S, 157°36.9′W, 2 February 1966, 140-200 m, USNM 729714. 1 female, ML 53 mm, TC-32, Stn. 22, 21°02′N, 158°29.7′W, 21 July 1967, 67-117 m, USNM 729723. 1 female, ML 45 mm, TC-32, Stn. 56, 21°22.4′N, 158° 14.6′W, 23 August 1967, 97-179 m, USNM 577609.

Other material: 1 specimen, ML 27 mm, HMS-47, Stn. 51, 00°44′S, 149°46′W, 2 November 1958, 576 m. 1 specimen, ML 12 mm, CHG-51, Stn. 164, 16°44′N, 169°16′W, 14 February 1961, 100 m. 1 specimen, ML 12 mm, CHG-51, Stn. 172, 19°21′N, 169°20′W, 15 February 1961, 0-100 m. 1 specimen, ML 16 mm, CHG-89, Stn. 29, 04°05′S, 167°51′W, 14 February 1966, 120-135 m. 1 specimen, ML 11 mm, CHG-89, Stn. 30, 02°59′S, 167°51′W, 15 February 1966, 100-125 m. 1 male, ML 46 mm, TC-32, Stn. 23, 21°00.2′N, 158°30.1′W, 22 July 1967, 17-25 m. 1 female, ML 60+ mm, TC-32, Stn. 28, 20°58.6′N, 158°33.7′W, 25 July 1967, 8-60 m. 1 female, ML 30 mm, 2 specimens, ML 12 and 19 mm, TC-32, Stn. 33, 20°58.8′N, 158° 28.4′W, 13 August 1967, 83-99 m. 1 female, ML 32 mm, 1 specimen, ML 22 mm, TC-32, Stn. 37, 20°59.1′N, 158°12.7′W, 15 August 1967, 55-123 m. 1 male, ML 30 mm, 2 females, 37 and 40 mm, TC-32, Stn. 38, 20°58.7′N, 158°27.9′W, 15

TABLE 4.—Measurements (in millimeters) and counts of *Enoploteuthis higginsi*. TC = RV *Townsend Cromwell*; CHG = RV *Charles H. Gilbert*; + = missing mantle tip and lost suckers.

Cruise:	TC-32	TC-32	TC-32	TC-32	*Teritu*	CHG-89	TC-32	CHG-51
Station:	28	22	23	56	6	11	56	172
Sex:	Female	Female	Male	Female	(Holotype) Male	Male	Female	?
Mantle length	60+	53	46	45	37	35	29	22
Mantle width	24	20	18	14	14	13	13	11
Head width	20	17	13	14	15	12	11	10
Fin length	—	39	30	34	27	23	20	15
Fin width	58	42	38	34	30	30	24	21
Arm length								
Right I	42	32	25	26	20	20	[1]13	15
Right II	24	36	27	25	20	21	[1]15	12
Right III	48	33	28	28	21	20	[1]15	12
Right IV	51	37	28	31	23	23	19	11
Left IV	53	34	32	33	23	—	17	13
Arm hooks/suckers								
Right I	26/22	25/34	19/—	25/22	20/16	24/16	16/19	16/20
Right II	29/27	26/34	22/—	25/20	22/16	23/20	17/20	18/20
Right III	32/28	28/33	22/—	25/22	22/20	22/20	18/23	16/21
Right IV	28/28	26/21	25/—	29/20	22/2+	26/14+	22/23	18/6
Left IV	28/26	27/20	27/—	29/22	26/16	—	20/23	20/7
Tentacles right/left								
Tentacle length	—	108/117	110/—	—/92	41/41	60/—	—/48	34/27
Club length	—	17/17	16/—	—/16	11/11	11.5/—	—/9	—
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	—	5/6-5/6	4/6-—	—-6/6	5/6-5/6	5/6-—	—-4/6	—
Club suckers right/left								
Distal suckers	—	68/68	—	—/60	60/60	72/—	—/64	—
Carpal suckers	—	3/3	3/—	—/3	3/2	3/—	—/3	—

[1] Length or count of left arm.

August 1967, 8-25 m. 1 male, ML 46 mm, TC-32, Stn. 41, 20°58.9′N, 158°29.1′W, 16 August 1967, 59-122 m. 1 female, ML 37 mm, TC-32, Stn. 44, 21°00.1′N, 158°29.1′W, 18 August 1967, 72-118 m. 1 female, ML 47 mm, TC-32, Stn. 45, 20°58.1′N, 158°28.7′W, 18 August 1967, 12-31 m. 2 specimens, ML 27 and 28 mm, TC-32, Stn. 46, 20°57.6′N, 158°28.7′W, 18 August 1967, 77-118 m. 1 female, ML 35 mm, TC-32, Stn. 48, 20°59.7′N, 158°27.7′W, 19 August 1967, 60-104 m. 1 female, ML 29 mm, TC-32, Stn. 56, 21°22.4′N, 158°14.6′W, 23 August 1967, 97-179 m.

Description: The muscular mantle is slender (MWI 31.1-*37.9*-44.8) and conical; the translucent tail is slender and ends bluntly. The ventral anterior edge of the mantle is not deeply excavated and the lateral angles are pointed, but low. The dorsal anterior lobe is low.

The fins are triangular, wide (FWI 75.6-*81.2*-85.7), and long (FLI 65.2-*70.4*-75.6). The anterior margin near its attachment is a rounded lobe, but more laterally it appears straight. The lateral angles (about 75°) are rounded at the tip. The slightly concave posterior margins join the mantle independently, but the union of both fins (close to the tip of the mantle) is indistinct.

The funnel is triangular and wide at the base. The funnel valve is a wide semicircular flap. The funnel organ is large; an anterior papilla and thick lateral ridges are present. The funnel-mantle locking cartilage is simple with a shallow groove. The anterior part of the cartilage is slightly narrower than the posterior end.

The head is as wide as the mantle (HWI 28.3-*34.0*-40.5). The eye opening is a wide oval with a deep anterior sinus. The funnel groove is moderately deep and the lateral sides continue posteriorly as sharp ridges. The ventral ocular "windows" are translucent. The three nuchal folds are very prominent. The tongue-shaped olfactory organ is attached to the first fold closest to the funnel. The second and third folds are united to each other posteriorly and the third fold on each side continues as a much reduced fold toward the dorsal midline.

The buccal membrane has a DDVD attachment to the arms. Numerous folds and broad tonguelike papillae occur on the inner surface of the membrane. The external surface is densely supplied with small purplish chromatophores so that it is darker than most parts of the body.

The arms are slender but muscular, nearly square in cross section at the base and finely pointed at their tips. The arms are moderate in length (ALI: I, 44.8-*54.8*-60.4; II, 51.7-*58.0*-67.9; III, 51.7-*58.5*-62.3; IV, 58.6-*65.5*-73.3). Arm IV is longest in both sexes. The swimming keels are developed to about one-half of arm I distally, two-thirds of arm II distally, and complete in arm III where they are as wide as the arm at the midsection. The lateral membrane (tentacular sheath) of arm IV is wide and reaches to the tip of the arm. Dorsal and ventral protective membranes are developed on all the arms of both sexes. They are widest on arm III and least developed on arm IV, except on the hectocotylized arm of the male.

The right ventral arm of the male is hectocotylized. The protective membranes of this arm are modified. At about the middle half of the arm opposite the sixth pair of hooks, the ventral protective membrane becomes enlarged into a wide undulating flap that is reduced abruptly about three-fourths of the arm length and continues distally to the tip of the arm as a much narrower membrane. The dorsal protective membrane, on the contrary, is only slightly modified. A short semilunar flap is present opposite the distal end of the larger ventral flap (Fig. 5F). Numerous conical papillae are scattered on the oral surface of the arms of males between the bases of the hooks and on the bases of the arms.

The arms have biserial hooks proximally and biserial suckers distally. The hooks (Fig. 5E) are strongly attached and completely enclosed by sheaths. About half of the suckers at the tips of the arms have long stalks and wide openings. The distal half of the inner rim of the sucker has seven to eight teeth; the two middle teeth are narrower than the lateral teeth; a shelf is visible on the proximal half (Fig. 5B). The outer ring bears numerous pegs. The remaining suckers gradually become smaller distally, assuming a globular shape with smaller openings that lack teeth and outer rings.

The robust tentacles are much longer than the mantle (TLI 110.8-*190.3*-239.1). The stalk near the base is almost square in cross section and as stout as arm III. The carpus and manus of the club are wide but the dactylus is quite narrow (Fig. 5G). The carpal cluster is compact and it includes three smooth-ringed suckers (very rarely two suckers) and several rounded pads and some elongate ridges and grooves; these are arranged in an oval cluster. Ten to 12 very robust, sheathed hooks are present in two rows

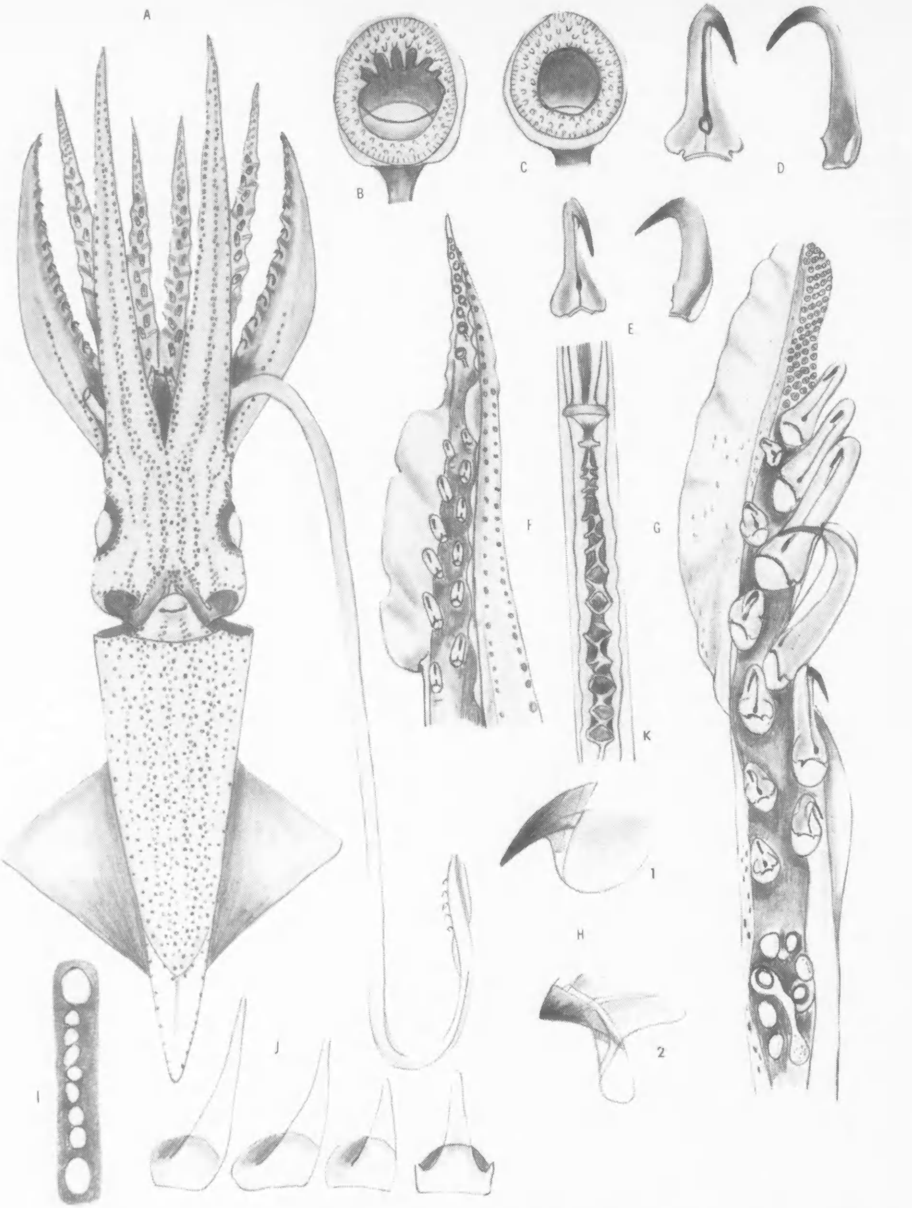


FIGURE 5.—*Enoploteuthis higginsi.* (A-E, G, and I from female paratype, ML (mantle length) 45 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm sucker; C, Tentacular sucker; D, Tentacular hook, oral and lateral aspects; E, Dorsal arm hook, oral and lateral aspects; F, Hectocotylus, male holotype, ML 37 mm; G, Tentacular club; H, Mandibles: upper (1), lower (2), female, ML 37 mm; I, Eye light organs; J, Radular teeth, female, ML 37 mm; K, Section of spermatophore, male, ML 46 mm.

on the manus. The ventral row includes a few large curved hooks, the largest hook is about one-fifth larger than the largest arm hook. The hooks have broad bases (Fig. 5D) and fit into shallow depressions on the club. The distal club suckers are arranged in four longitudinal rows (between 15 and 18 suckers in each row). The inner rings of these suckers are smooth but are surrounded by an outer ring with broad pegs that can be mistaken for teeth of the inner ring (Fig. 5C). A few suckers in the distal part of the dactylus are slightly enlarged and form a cluster there at the blunt end of the club. The dorsal or aboral keel is well developed and extends from opposite the third dorsal hook to the blunt end. A smaller semilunar membrane lies on the oral or ventral side of the club. It extends from opposite the distal half of the carpal cluster to opposite the second or third ventral hook. Protective membranes are poorly developed but recognizable.

The integumentary photophores range in size from about 0.2 mm to about 0.4 mm with varying degrees of pigmentation. Some are very dark with small pearl gray centers, others are lighter with varying widths of peripheral pigmentation. Those with very thin dark rings appear palest or almost white. The photophores on the ventral surface of the mantle appear to be distributed at random (Fig. 5A). They are concentrated on the ventral surface except at the tail and gradually become widely scattered toward the dorsal surface. A single row extends along each lateral margin of the tail. The free edge of the mantle opening is lined by a transverse row where the photophores are farther separated dorsally. There are no photophores on the fins, or on most of the ventral area of the tail.

Two rows of photophores separated by a median space are present on the ventral surface of the funnel. A shorter row or patch occurs on each of the lateral margins and a wider strip is found on each of the dorsolateral surfaces of the funnel.

The distribution of the photophores on the head is rather intricate. A small cluster lies in the apical region of the funnel groove. The ventral midline of the head is not totally clear of light organs, as a few isolated ones may be present. A very short row of three to four photophores in single file on the ventral midline (near the bases of arm IV) splits into two at the fork of the arms; each branch then continues along the ventral aboral edge of arm IV, ending a short distance from the distal tip of the arm. A row of photophores begins near the first nuchal fold, follows the curve of the funnel groove, and at a point near the apex of the funnel groove it splits into a wider medial branch and a narrower lateral branch. These branches reunite near the base of arm IV and the combined row proceeds anteriorly along the base of the tentacular sheath to the tip of arm IV. The next lateral row begins anterior to the first nuchal fold, is interrupted by a gap at the window of the eye, continues for a short distance, and divides into two short branches; each branch then extends to the edge of the tentacular sheath independently. A row of single photophores runs along the edge of the tentacular sheath and stops a short distance from the tip of arm IV. The lateralmost row on the head extends from the first nuchal fold along the nuchal crest, then anteriorly to and along the ventral margin of the eyelid, and ends at the ventral edge of the optic sinus. The row begins again on the dorsal edge of the optic sinus, continues along the base of the swimming keel of arm III, and terminates at about one-half the length of the arm. Two or three isolated small photophores occur in the area surrounding the ventral part of the eye opening; one photophore is usually located directly lateral to the window.

There are nine light organs on the ventral part of the eyeball. The terminal organs are much larger and slightly separated from seven smaller, closely set, light organs (Fig. 5I).

The radular teeth (seven teeth in a series) are long and slender. The outermost lateral teeth are longest while the innermost lateral teeth are shortest. The rachidian tooth has cusps. The three median teeth are almost straight while the two outermost lateral teeth are slightly curved (Fig. 5J).

The upper mandible (Fig. $5H_1$) has a pointed rostrum with very sharp edges and the lower mandible (Fig. $5H_2$) has three well-developed ribs on the gular plate.

The gladius is feather shaped and the midrib is low and rounded. The cone is narrow and rounded at the extreme end. The vanes start to broaden at about one-third of the length and reach their greatest width at about half of the length. The lateral edges of the gladius appear slightly thickened when held against a strong light.

Spermatophores from a male (ML 46 mm) are about 14 mm in total length. The cement body is slightly greater than half the length of the sperm reservoir and has two collars at the oral end (Fig.

5K), the anterior much smaller than the posterior. The aboral part of the spiral filament is supplied with numerous intricate diamond-shaped depressions separated by thickened ridges. Two to four turns are present behind the cap. A spermatophore examined has the following measurements:

Spermatophore segment	*Length (mm)*
Entire spermatophore	13.8
Sperm reservoir	5
Cement body	2.8
Spiral filament	6.0

Some eggs taken from the ovary of the female paratype (ML 53 mm) measured about 1.2 mm each.

Young individuals: Small individuals (ML 11-16 mm) have relatively wider mantles (MWI 56.3-*59.4*-63.6) and the photophores on the mantle are scattered (Fig. 2E) as they are in the adult. At ML 15 mm all the rows of photophores on the head correspond to those of the adult with respect to number and position (Fig. 2G). The most medial row consists of several photophores set close to each other as in the adult. All other rows are composed of a single line of photophores. At ML 12 mm the tentacles are robust and longer than the mantle (TLI 108.3), more than the length of the arm. The club has two carpal suckers, four hooks on the ventral side of the manus among a group of 16 suckers (presumably future hooks), some marginal suckers, and numerous quadriserially arranged suckers on the dactylus. The aboral keel is also developed. The arms bear between 12 and 14 hooks and a sucker at the base of one of the dorsal arms. Thirteen or 14 suckers occupy the distal part of arms I, II, and III, and 24 suckers on arm IV. At ML 16 mm there are still 4 club hooks and 2 carpal suckers, but the arm hooks have increased (18 on arm IV) as have the distal suckers. At ML 19 mm, 16 to 19 hooks are observed on the arms and 6 to 7 on the club along with an increased number of distal arm suckers and club suckers. At this stage three carpal suckers are present as in the adult.

Remarks: The species can be easily confused with *E. jonesi*; counts and measurements overlap and both species can be found in the same trawl hauls. However, a close examination of the material reveals a series of minor but consistent characteristics that separate one from the other even at a small size (ML 10 mm). At comparable sizes the tentacles and clubs are similar in structure, but *jonesi* has 13 or 14 club hooks and usually 4 carpal suckers while *higginsi* has 11 or 12 club hooks and usually 3 carpal suckers. Both have long tentacles, but they are relatively longer in *higginsi*.

Discrete longitudinal arrangement of photophores on the mantle is wanting in *higginsi* while a median space and identifiable rows are found in *jonesi*. The arrangement of photophores on the head also shows some differences: 1) The row closest to the midline is multiserial in *higginsi* whereas it is simple in *jonesi*; 2) isolated photophores occur in the midline area of the head and in the space near the eye in *higginsi* but are absent in *jonesi*; 3) the row directly anterior to the window is bifurcate in both species but in *higginsi* both branches extend to the tentacular sheath whereas in *jonesi* only the lateral branch does; and 4) the row of photophores on arm III is incomplete in both species, but in *higginsi* the row rarely extends more than 50% of the arm length (45-52% of arm length, 11 specimens) and in *jonesi* the row is more than half the arm length (56-85% of arm length, 18 specimens).

Enoploteuthis higginsi, like *E. jonesi*, shares many characteristics with *E. chuni* and *E. anapsis* (see remarks section of *E. jonesi*), but the scattered distribution of photophores on the mantle is distinctive of *higginsi*. Rows do not occur on the mantle in any stage of development in *higginsi*. At ML 10 mm, or smaller, the rows are already evident in *anapsis* (Roper 1966, figs. 22, 23).

Specimens captured in Hawaiian waters which were labeled *Enoploteuthis* sp. B and reported in Young (1978) also belong to this species (R. E. Young[3]).

This enoploteuthid squid is named after Bruce E. Higgins, former fishery biologist at the Honolulu Laboratory under whose leadership most of the material was collected during cruise 32 of the RV *Townsend Cromwell* in Hawaiian waters.

Distribution: Central Pacific, Hawaiian, and equatorial regions.

---

[3] R. E. Young, Department of Oceanography, University of Hawaii, Honolulu, HI 96822, pers. commun. 3 March 1980.

Enoploteuthis reticulata Rancurel 1970

(Figs. 6, 2B; Table 5)

Enoploteuthis reticulata Rancurel 1970: figures 31-37 (incorrect spelling *reticula* in figures 31-33).

Enoploteuthis sp. (No. 1), Okutani, 1974: figures 12a, b, e.

Enoploteuthis sp. A, Young 1978: figures 9B, 10A.

Material examined: 1 male, ML 130 mm (regurgitated by a porpoise) CHG-7, 20°42.7′N, 157°50′W, 3 February 1953, USNM 729718. 1 male, ML 117 mm, HMS-30, Stn. 3, 28°38.5′N, 161°20.3′W, 16 July 1955, 100 m. 1 specimen, ML 26 mm, TC-7, Stn. 5, off Waianae, Oahu, 12 August 1964, 60-100 m. 1 female, ML 35 mm, TC-32, Stn. 3, 21°22.5′N, 158°13.5′W, 13 July 1967, 15-25 m. 1 specimen, ML 13 mm, TC-32, Stn. 4, 21°20.9′N, 158°13.1′W, 13 July 1967, 75-107 m. 1 specimen, ML 18 mm, TC-32, Stn. 6, 21°21.7′N, 158°13.3′W, 14 July 1967, 83-124 m. 1 female, ML 45 mm, TC-32, Stn. 9, 21°21.5′N, 158°13.5′W, 15 July 1967, 17-25 M. 2 females, ML 39 and 62 mm, TC-32, Stn. 15, 21°20.3′N, 158°12.2′W, 17 July 1967, 16-30 m, USNM 729691. 1 specimen, ML 30 mm, TC-32, Stn. 28, 20°58.6′N, 158°33.7′W, 25 July 1967, 92-122 m. 1 male, ML 46 mm, TC-32, Stn. 29, 20°59.5′N, 158°31.5′W, 26 July 1967, 8-60 m. 1 male, ML 71 mm, TC-32, Stn. 31, 20°59.6′N, 158°29.3′W, 13 August 1967, 80-121 m, USNM 577606. 1 specimen, ML 32 mm, TC-32, Stn. 46, 20°57.6′N, 158°28.7′W, 18 August 1967, 77-118 m. 1 male, ML 50 mm, TC-32, Stn. 48, 20°59.7′N, 158°27.7′W, 19 August 1967, 60-104 m.

Description: The mantle is almost circular in cross section and is very muscular; the tail is thin and translucent. The mantle is widest at the opening (MWI 27.4-*32.3*-37.1) and the sides converge gradually toward the saccate tail. The anterior ventral margin is very slightly excavated and the lateral angles are pointed, but low. The dorsal evagination of the mantle is a rounded and low lobe.

The fins are about three-fifths of the mantle length (FLI 62.4-*64.7*-67.7) and are moderately wide (FWI 59.8-*69.3*-82.6). They arise at about the anterior third of the mantle length. The anterior margin projects as a rounded lobe near its attachment and then extends laterally, and together with the almost straight posterior margin, a rounded angle (about 72°) is formed. The posterior margins are each joined to the mantle separately leaving a small gap between them.

The funnel is triangular and almost as wide as

TABLE 5.—Measurements (in millimeters) and counts of *Enoploteuthis reticulata*. CHG = RV *Charles H. Gilbert*; HMS = RV *Hugh M. Smith*; TC = RV *Townsend Cromwell*; + = missing arm tips and lost suckers.

Cruise:	CHG-7	HMS-30	TC-32	TC-32	TC-32	TC-32	TC-7	TC-32
Station:		3	31	15	29	28	5	6
Sex:	Male	Male	Male	Female	Male	?	?	?
Mantle length	130	117	71	62	46	30	26	18
Mantle width	38	32	22	23	17	12	11	10
Head width	31	30	19	17	13	12	8	8
Fin length	88	73	43	42	30	16	15	9
Fin width	85	70	48	44	38	20	18	14
Arm length								
Right I	65	58	[1]45	35	28	17	15	12
Right II	65	65	[1]46	43+	30	19	15	13
Right III	70	[1]60	[1]47	34+	30	18	16	12
Right IV	69	65	45	38	33	18	17	13
Left IV	72	66	48	40	31	19	17	13
Arm hooks/suckers								
Right I	26/—	24/8+	[1]21/24	21/20	20/15	20/11	21/14	21/14
Right II	24/—	24/19	[1]23/24	26/16	20/18	18/10	21/12	20/15
Right III	24/—	24/22+	[1]24/15	24/14	22/13	20/11	22/11	21/14
Right IV	32/—	34/17	33/20	28/11	29/9	27/12	30/9	30/10
Left IV	31/—	33/19	33/35	31/12	26/13	27/12	28/10	30/9
Tentacles right/left								
Tentacle length	120/126	93/115	76/68	80/60	47/49	22/28	20/20	—/16
Club length	20/20	21/21	16/16	—/14	14/14	8/8	6/6.5	—/5
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	5/5-4/5	5/6-5/6	6/6-7/5	5/5-5/5	5/6-4/5	5/5-5/5	4/5-5/5	—-3/5
Club suckers right/left								
Distal suckers	—	10/8	10/8	—	11/8	8/—	10/9	—/8+
Carpal suckers	5/4	4/6	6/6	5/5	5/5	4/6	5/7	—/6

[1] Length or count of left arm.

it is long. The funnel-mantle locking cartilage is simple. The anterior end is slightly pointed and narrower than the posterior end. The groove is shallow and wider posteriorly. The funnel organ has a papilla on the anterior end of the dorsal component (inverted V-shape), is small, and has wide ridges on the lateral limbs. The ventral components are oval but have pointed anterior ends. The funnel valve is broad and its rounded anterior edge reaches the level of the funnel opening.

The head is almost square in cross section, slightly rounded at the top, and narrower than the mantle (HWI 23.8-*26.4*-28.3). The ventral excavation is moderately deep and well marked by sharp lateral edges. The three nuchal folds on each side of the head are very prominent. The first nuchal fold bears a tonguelike olfactory papilla at its posterior end. The second and third folds are crescentic folds with broad anterior ends and are united to each other posteriorly by a narrow membrane. From the posterior end of the third fold a narrow membranous ridge extends toward the dorsal midline but does not quite reach it. In large specimens the nuchal crest connects the three folds to each other and to the midline, so that three oval areas are formed on each side of the head posteriorly. The eye opening is wide and has a deep sinus. Both dorsal and ventral ocular "windows" are easy to recognize, particularly in specimens that have been preserved longer.

The buccal membrane has eight stout supports with connectives attached to the arms in the order DDVD. The lappets are pointed and the inner surface of the buccal membrane is rugose and lacks papillae. The membrane is darker than the supports; small chromatophores are present in both structures.

The arms are moderate in length; the ventral arms, which are longest, are shorter than the mantle length (ALI: I, 49.7-*56.1*-63.4; II, 50.0-*58.9*-65.2; III, 51.3-*59.1*-66.2; IV, 53.1-*61.7*-71.7). Weak keels extend along the distal third of arm I, along the distal half of arm II, and from the base to the tip of arm III. In the largest specimen the swimming keel of arm III is slightly wider than the arm width. The tentacular sheath along arm IV is narrow, about half of the arm width near the base, and reaches the tips of the arms. The protective membranes are developed on borders of all arms, but are more strongly developed on the ventral borders. This is particularly so on arm III, although the ventral membrane is never wider than the height of the hooks. The trabeculae and the membranes are very distinct even at the tips of the arms.

The right ventral arm of the male is hectocotylized (Fig. 6B). The ventral protective membrane on this arm is enlarged into an undulating lappet, which extends from near the 9th or 10th pair of hooks to the arm tip, although it becomes progressively reduced in width distally. The membrane is deeply notched at about two-thirds of its length so that two semilunar flaps of unequal lengths are formed. The dorsal protective membrane is less developed than the ventral protective membrane even in the area opposite the enlarged lappet. In addition, the males have numerous conical tubercles distributed on the oral surface, at the bases of all the arms, and on the areas between the bases of the hooks.

The arm hooks are large (Fig. 6E), arranged in two alternate rows, and enclosed by sheaths. The ventral arms of both sexes bear the most hooks. None of the hooks are unusually enlarged or reduced in either sex. The distal part of each arm has two rows of suckers. The proximal suckers in this region have long stalks and the inner rings of these suckers have seven or eight large blunt teeth (middle two teeth broadest) distally and smooth proximally (Fig. 6C). The outer ring has long pegs. The most distal pairs of suckers (with about three teeth) are much reduced in size, carried on short stalks, and have small openings.

The tentacles are generally about the length of the mantle (TLI 79.5-*100.4*-129.0). The stalk is slender, only about one-third of the width of arm III. The sides are compressed and the cross section is almost triangular. The club is narrow (Fig. 6I). The carpus includes between four and seven smooth-ringed suckers and corresponding pads arranged in an elongated series which is limited on both sides by a narrow ridge. The manus includes a dorsal row of four to seven sheathed hooks and a ventral row of five or six slightly larger hooks. The hooks (Fig. 6F) have narrow bases. The largest hooks are not bigger than any of the largest arm hooks. Marginal suckers are absent and any sucker present along the rows of hooks in young specimens certainly represents an undeveloped hook. The dactylus has 8 to 11 suckers arranged in two rows. They have long stalks and wide openings. The sucker rings bear teeth; six or seven short teeth distally and six or seven very blunt teeth proximally (Fig. 6D). The outer ring has many short pegs. The tip of the club is blunt with a short over-

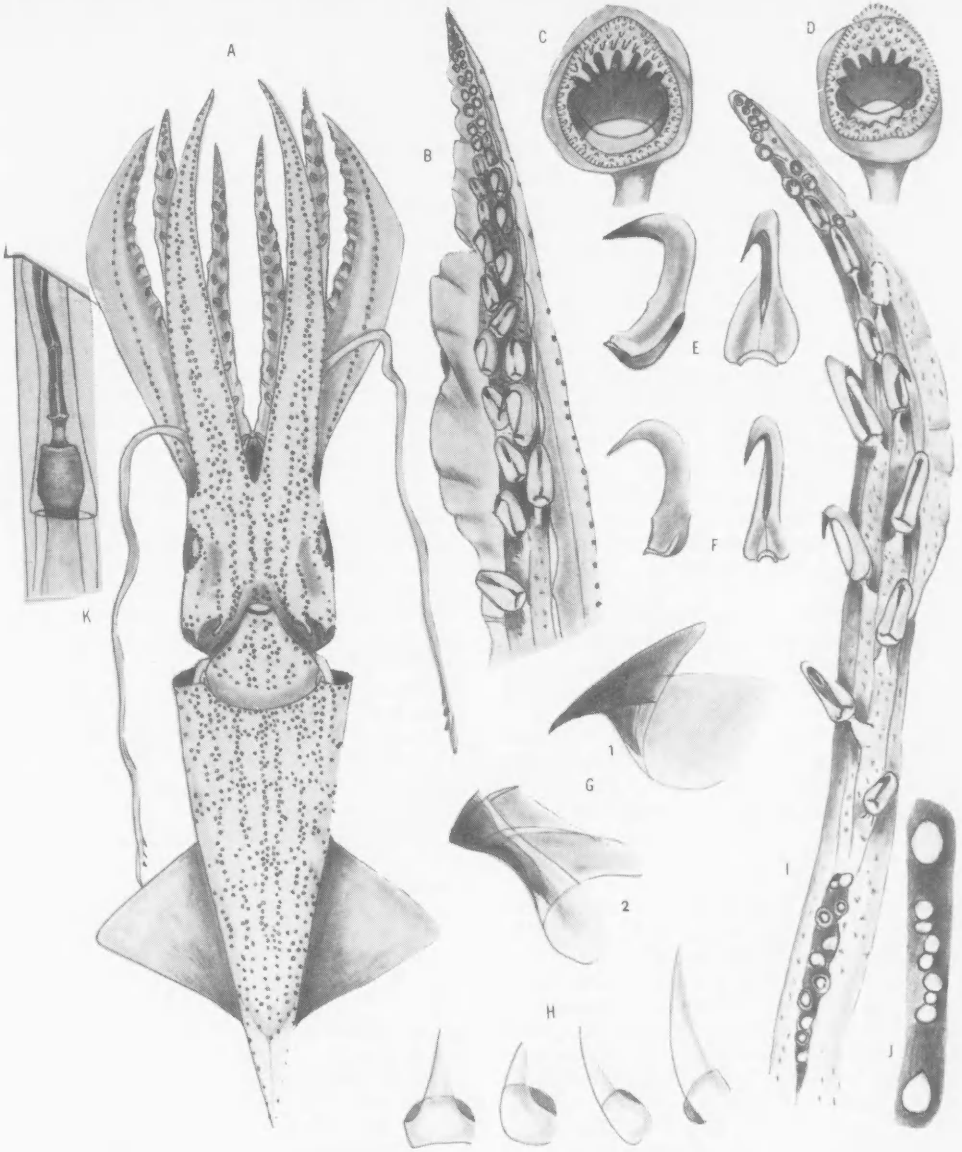


FIGURE 6.—*Enoploteuthis reticulata* Rancurel. (A, C-F, and J from female, ML (mantle length) 62 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Hectocotylus, male, ML 71 mm; C, Dorsal arm sucker; D, Tentacular sucker; E, Dorsal arm hook, oral and lateral aspects; F, Tentacular hook, oral and lateral aspects; G, Mandibles: upper (1), lower (2), male, ML 50 mm; H, Radular teeth, male, ML 50 mm; I, Tentacular club, male, ML 117 mm; J, Eye light organs; K, Section of spermatophore, male, ML 117 mm.

lapping hood which conceals a few of the suckers at the tip. The aboral keel is also narrow and extends from opposite the second hook to the lateral side of the hooded tip. Protective membranes are not developed on either side.

The photophores range in size from 0.2 to 0.4 mm. The dark or light appearance of each photophore is caused by the extent of pigmentation. The majority of the small ones are white owing to pigmentation confined only to the periphery of the photophores. The photophore pattern of the mantle is distinctive. It can be described briefly as the combined effect of about six ill-defined longitudinal rows and four oblique rows to produce a netlike or reticulated pattern (Fig. 6A). The photophores are scattered irregularly in the posterior region of the mantle, except on the tail where a single row extends on each side to the tip of the tail. The ventral area of the saccate tail lacks photophores. A single transverse row in which the photophores are farther apart dorsally lies along the anterior edge of the mantle. A few small photophores are distributed on the dorsal surface of the mantle. The fins lack photophores.

Two longitudinal rows, separated by a midline space, occur on the ventral surface of the funnel. A short row (connected to the ventral row posteriorly) is located on each side of the funnel and a long row of photophores is found on the dorsolateral side, close to each bridle.

The photophore pattern on the ventral side of the head is observed best in smaller specimens. Two clusters, separated by a narrow midline space, lie in the apex of the funnel groove. A clear space occupies the ventral midline of the head. Eight main rows of photophores (four rows on each side of the midline space) are present. The first or most medial row begins at the posterior end of the funnel groove, extends anteriorly to the ventral aboral side of arm IV, and reaches almost to the tip of this arm. The second row branches out from the first row near the apex of the funnel groove, extends parallel to the first row and joins it at a point near the base of arm IV, at about the same level as the anterior margin of the eye. At the base of arm IV the width of the second row is increased by additional photophores, and as the row continues along the base of the tentacular sheath distally it is gradually reduced to a single series of photophores which reaches the tip of the arm. A very short row or cluster of photophores occurs between the first and second rows at a short distance beyond the base of arm IV, but in older individuals this short row tends to lie closer to the second row and may be difficult to distinguish. The third lateral row extends from opposite the first nuchal fold anteriorly (interrupted by a gap at the window of the eye) to the base of arm IV where it merges with the second row. A branch continues further along the edge of the tentacular sheath almost to the tip of arm IV. The fourth or most lateral row extends from the second nuchal fold to the posterior margin of the eye and passes along the edge of the ventral eyelid to the ventral edge of the optic sinus. The row begins again on the dorsal edge of the optic sinus and continues along the base of the swimming keel of arm III to a short distance from the tip. An arclike row of small white photophores, spaced widely, lies along the ventral region of the eye between the third and fourth rows of photophores.

Nine light organs, arranged in a single row, are present on the ventral side of the eyeball. The terminal organs are much larger than the seven, closely spaced, interior light organs and are set apart from them. The interior organs are not of uniform size (Fig. 6J).

The seven radular teeth are blunt and slightly curved. The rachidian has low lateral cusps (Fig. 6H).

The mandibles are strong; the rostrum of the upper mandible is pointed and the edges are sharp (Fig. $6G_1$). The gular plate of the lower mandible is reinforced by three stout ribs (Fig. $6G_2$). At ML 45 mm the wings of both halves are already well pigmented.

The gladius is thin with a low rounded midrib. The vanes are narrow and widest at about the middle. The cone is thin-walled and as wide and rounded as the anterior end of the gladius.

The spermatophores are large. The cement gland has a large swelling at the aboral end (Fig. 6K). The aboral end of the spiral filament, anterior to the cement gland, is plain except for some longitudinal ridges. Two or three spiral turns behind the cap are present. Measurements from two specimens are given below:

	Length (mm)	
Spermatophore segment	*ML 130 mm specimen*	*ML 71 mm specimen*
Entire spermatophore	28	14
Spiral filament	12	6.2
Cement gland	3	1.8
Sperm reservoir	13	6

Young individuals: At ML 13 mm the photophores on the mantle are arranged as small clusters of large photophores distributed in a definite pattern (Fig. 2Ba). There are a few small and large photophores on the head, arms, and funnel, and they are aligned in areas that correspond to the adult pattern. At this stage there are 17 to 21 arm hooks and 7 to 11 distal arm suckers. The tentacles are shorter than the mantle (TLI 84.6) and weak. On the club a single hook, along with 16 suckers in two rows, is developed; however, the carpal area is not yet differentiated. At ML 18 mm, 20 or 21 hooks and 14 or 15 distal suckers are present on each of arms I, II, and III, and 30 hooks and 9 distal suckers are present on arm IV. On the club, 6 carpal suckers are set apart from 8 hooks (biserial) on the manus and about 13 suckers on the dactylus. At ML 26 mm the photophore pattern of the mantle appears more complex. First, additional photophores develop between the clusters whereby four oblique rows are present; and second, six longitudinal rows of indistinct small white photophores are present (Fig. 2Bb). This pattern, although not as complicated, resembles that of the adult. At this stage the clubs have 9 or 10 hooks, 9 or 10 distal suckers (biserial), and 5 to 7 carpal suckers. A ML 45 mm female has an oviducal gland 2.0 mm long, and at ML 46 mm the right ventral arm of the male is already hectocotylized, although the lappet is still very narrow and the tubercles on the arm bases are minute. There is no indication of spermatophores in the still undeveloped genital system. However, a ML 50 mm specimen has spermatophores.

Remarks: The present material can be assigned with confidence to *E. reticulata* (Rancurel 1970). The photophore patterns of the mantle, head, and arms, and characteristics of the tentacles and clubs are very close, and hook counts (arms and clubs) overlap. Differences in measurements are not considered to be significant.

Okutani (1974; 51, fig. 12a, b, e) described and illustrated a specimen, labeled n. sp. (No. 1) in his paper on the cephalopods collected at lat. 17°53′S, long. 126°18′W during the EASTROPAC Expedition, 1967-68; I have examined this particular specimen deposited in the U.S. National Museum; it is *E. reticulata*.

Enoploteuthis sp. A of Young (1978) belongs to *E. reticulata* described here (R. E. Young footnote 3).

The reticulated pattern is not unique. A similar pattern has been described for *E. galaxias* Berry, 1918. However, these two species differ in a number of basic features. Except for the mantle photophores, the pattern of the light organs in *galaxias* is unlike that of *reticulata*; there is a median row present in the head of *galaxias* flanked by three lateral rows, or a total of seven rows. A median row is absent in *reticulata*. I have examined the type of *E. galaxias* deposited at the Australian Museum, Sydney, Australia. Unfortunately, the specimen has darkened considerably and the photophore pattern is no longer recognizable with an ordinary microscope. The tentacles and clubs are very different. The tentacular stalk in *galaxias* is as stout as the arms, but in *reticulata* the stalk is only a third of the arm width. The club of *galaxias* has an expanded carpus, whereas in *reticulata* the carpus is very slender. The carpal suckers and pads in *galaxias* are arranged in a compact oval area, but in *reticulata* they are biserially arranged lengthwise in a narrow area. The suckers of the dactylus in *galaxias* are quadriserially arranged and quite numerous (38-43), whereas they are biserially arranged and very few (8-11) in *reticulata*. Lastly, the rachidian tooth of *galaxias* has no cusps, but that of *reticulata* does.

The present collection data and those from the literature show that *E. reticulata* occurs over a wide area of the Pacific, Hawaiian waters included, from lat. 28°38.5′N to 22°58′S and from long. 164°04′E to 126°18′W.

GENERAL DISCUSSION

Since the description of *Loligo leptura* by Leach (1817) and the subsequent designation of this species as the type of the genus *Enoploteuthis* Orbigny, 1848 by Pfeffer (1900), only five other valid species have been described: *E. chuni* Ishikawa 1914; *E. galaxias* Berry 1918; *E. anapsis* Roper 1964; *E. theragrae* Taki 1964; and *E. reticulata* Rancurel 1970. (See summary of history, synonymy, and generic diagnosis in Roper 1966.)

Enoploteuthis dubia Adam 1960 was described from a single specimen captured in the Gulf of Aqaba, Red Sea. However, Adam in his remarks was not certain that it was an *Enoploteuthis*. With more material and information several years later, he removed the species from *Enoploteuthis* (Adam 1973).

Enoploteuthis theragrae was described from seven specimens found in the stomach contents of two codfish, *Theragra chalcogramma*, captured in 1957 and 1962 from two localities in the Japan Sea. These specimens probably are allied to *E. chuni*. Except for the mantle photophores (six in rows for *theragrae* and eight in rows for *chuni*) all other diagnostic characters are shared by both species (M. Okiyama[4]).

GEOGRAPHIC DISTRIBUTION

Enoploteuthis anapsis and *E. leptura* are widely distributed in the Atlantic. *Enoploteuthis leptura* is known from the Gulf of Guinea (type locality), Madeira, Cape Verde Islands, the southern Straits of Florida (Roper 1966), and east of Bermuda (Roper 1977). *Enoploteuthis anapsis* is recorded from parts of the western Atlantic in the Gulf of Mexico and Caribbean Sea, from the mid-Atlantic, Madeira, St. Helena, and South Equatorial Current (Roper 1966), and east of Bermuda (Roper 1977).

Enoploteuthis chuni was first described from Toyama Bay, Sea of Japan, and Sasaki (1920) reported it later, again from Toyama Bay and farther south from Bungo Strait. Shimomura and Fukataki (1957) recorded it again from the sea of Japan together with *Watasenia scintillans* in the stomach contents of Alaskan pollock. Okutani (1967) listed an adult specimen from Sagami Bay on the Pacific side of Japan and some larval stages later (1968), also from the Pacific side of Japan. The first and only record of *E. theragrae* is from the Sea of Japan in 1964.

Enoploteuthis galaxias is known only from the type locality, off Gabo Island to Everard Grounds, Victoria, Australia.

Enoploteuthis reticulata was described from specimens taken by midwater trawl and from stomach contents of *Alepisaurus ferox* caught in areas of the southwest Pacific, approximately between lat. 22° and 18°S and long. 164°E and 133°W. The present material extends the distribution to lat. 21°N in the Hawaiian area and Okutani's specimen (1974, *Enoploteuthis* sp. No. 1) to the southeast Pacific at lat. 17°S, long. 126°W.

The genus *Enoploteuthis* was first reported from the central Pacific by King and Ikehara (1956) in their study of the food and feeding habits of the yellowfin tuna and bigeye tuna. They found a total of 36 specimens of *Enoploteuthis* in the stomach contents of these fishes. There are no other previous records of the genus from the central Pacific. The station data of the present material show that *E. obliqua* ranges approximately from lat. 11°N to 5°S and long. 81° to 144°W; *E. octolineata* from lat. 7°N to 3°S and long. 144° to 157°W; *E. jonesi* from lat. 20°N to 14°S and long. 157° to 168°W; and *E. higginsi* from lat. 21°N to 4°S and long. 149° to 169°W. Of the five species found in the central Pacific, namely, *obliqua*, *octolineata*, *jonesi*, *higginsi*, and *reticulata*, the last three species range to areas close to the Hawaiian Islands whereas *obliqua* and *octolineata* do not (Fig. 7). Based on available records, *reticulata* has the widest range; it is found in the southwest Pacific, Hawaiian area, and southeast Pacific. Collections made between September 1969 and November 1974 by the University of Hawaii include specimens of *E. reticulata* and *E. higginsi* (Young 1978).

BATHYMETRIC DISTRIBUTION

The genus *Enoploteuthis* is rare in collections, and, except for *E. anapsis* (Roper 1966), *E. higginsi*, and *E. reticulata* (Young 1978), few depth records are available.

Useful depth data are available for only two specimens of *E. leptura* studied by Roper (1966). These specimens were taken from depths between 0 and 170-300 m. *Enoploteuthis anapsis* is represented by 25 specimens taken from depths between 33 and 600 m at night and a single specimen from very deep waters, 2,000 m, during the day. Roper and Young (1975) mentioned the capture of an *E. anapsis* specimen in a closing net at 90 m, off Bermuda at night.

Depth records are not included in the original description of *E. chuni*; however, the *Albatross* specimens reported by Sasaki (1920) came from the stomach of a fish captured from deep water, about 857 m. Okutani (1967, 1968) reported an adult from a depth of 700 m and two larval stages from the surface.

The only known specimens of *E. galaxias* (four specimens) were captured at depths between 288 and 450 m.

The present material, except for that from two tows at 240 and 576 m, came from depths between the surface and 179 m. Depth data and other pertinent records are listed in Table 6 for 131 specimens of *obliqua*, *octolineata*, *jonesi*,

---

[4] M. Okiyama, Tokyo University, Tokyo, Japan, pers. commun. 26 November 1970.

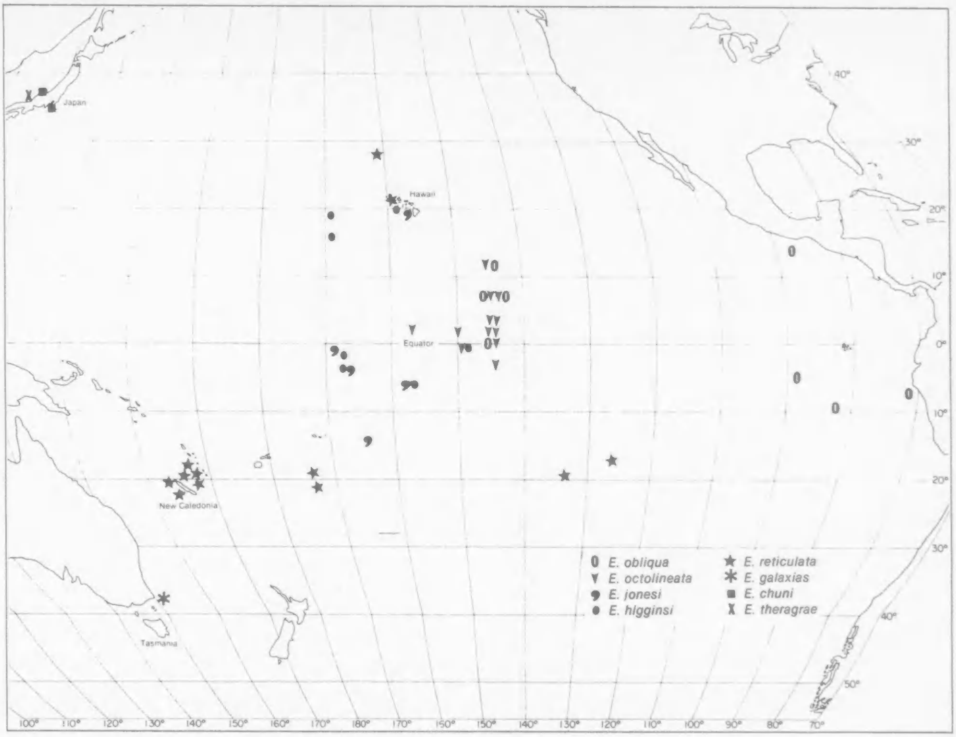

Japan
Hawaii
Equator
New Caledonia
Tasmania
0 E. obliqua
▼ E. octolineata
E. jonesi
● E. higginsi
★ E. reticulata
✱ E. galaxias
■ E. chuni
X E. theragrae
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
100°
110°
120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°

FIGURE 7.—Distribution of *Enoploteuthis* species in the Pacific.

higginsi, and *reticulata*. Most of the specimens (93.1%) were taken between the surface and 150 m, and the greatest number of these (48.1%) came from a depth of 50 m. A majority of the specimens (70.2%) were collected at night between 1900 and 0400. A limited number of specimens (8.4%) came from the few tows made during the day. *Enoploteuthis higginsi* and *E. reticulata* captured off Oahu, Hawaii, were taken close to the surface (50-100 m) at night and much deeper (500-600 m) during the day (Young 1978).

Species of *Enoploteuthis* are undoubtedly mesopelagic forms (200-1,000 m day habitat) that make diel vertical migrations as has been demonstrated for *E. anapsis* by Roper (1966) and for two other *Enoploteuthis* by Young (1978).

RELATIONSHIPS

The Pacific species of *Enoploteuthis* fall into two natural groups allied either to *E. anapsis* or *E. leptura* along the same characters that separate these two Atlantic species (see Roper 1966). Apparently, there are two species complexes within the genus: Species that tend toward the development of larger clubs and long and muscular tentacles, and those species that exhibit the opposite trends.

Additional features of the former complex are: many suckers in four rows on the clubs, large hooks, and oval to round carpal apparatus. These are features common to *galaxias*, *chuni*, *theragrae*, *anapsis*, *jonesi*, and *higginsi*. Within this group, *anapsis*, *jonesi*, and *higginsi* all have the semilunar membrane on the club while *galaxias* and *theragae* are illustrated in the literature without it. Both Berry (1918) and Taki (1964) do not mention the semilunar membrane in their species descriptions. I have seen the holotype of *galaxias*, but I could not verify the presence of the membrane because of the poor

TABLE 6.—Bathymetric data of *Enoploteuthis* species: *obliqua*, *octolineata*, *jonesi*, *higginsi*, and *reticulata*. TC = RV *Townsend Cromwell*; HMS = RV *Hugh M. Smith*; CHG = RV *Charles H. Gilbert*.

Cruise no.	Station no.	No. of specimens	Mantle length (mm)	Sex	Depth (m)	Time 24 h	Month
Enoploteuthis obliqua							
TC-48	19	1	58	M	50	—	April
TC-48	11	1	55	M	50	—	March
TC-46	9	1	50	F	50	1945-0230	October
TC-44		[1]1	50	F	—	—	July-August
TC-46	9	1	41	M	50	1945-0230	October
TC-48	19	1	40+	F	50	—	April
TC-44	24	1	37+	M	50	1933-0245	July
TC-44	17	[1]1	27	—	—	—	July
TC-44	24	4	12-20	—	50	1933-0245	July
TC-43	14	16	5-18	—	50	1945-0235	May
TC-43	22	5	12-17	—	50	2017-0237	May
TC-43	10	5	12-17	—	50	1943-0239	May
TC-44	18	2	12-17	—	100	1947-0253	July
TC-44	32	1	13	—	50	1937-0303	July
TC-44	54	1	12	—	50	1932-0238	July
TC-47	16	4	6-11	—	50	1930-0250	January
TC-48	16	3	7-10	—	20	—	April
TC-44	16	2	55-10	—	0	1059-0129	July
Enoploteuthis octolineata							
TC-43	52	1	75	F	50	1940-0244	May
HMS-47	58	1	71	F	212	2013-2153	November
TC-46	47	1	56	F	115	1939-0240	October
TC-46	37	1	56	F	50	1934-0236	October
TC-48	50	1	49	F	50	—	April
TC-48	52	1	46	M	50	—	April
TC-43	42	2	21-40	—	50	1942-0235	May
TC-48	35	1	39	—	50	—	April
TC-46	41	1	36	—	50	1935-0230	October
TC-48	92	1	33	—	50	—	April
TC-43	38	3	19-30	—	50	1944-0240	May
TC-44	44	[1]1	28	—	—	1935-0237	July
TC-44	26	1	26	—	20	1934-0243	July
TC-44	68	1	25	—	75	1932-0235	August
HMS-47	58	1	25	—	212	2013-2153	August
TC-43	48	1	24	—	50	1943-0240	May
TC-43	52	2	20-22	—	50	1940-0244	May
TC-43	26	1	20	—	50	1945-0235	May
TC-44	56	1	20	—	50	1933-0235	July
TC-47	45	2	16-20	—	50	2000-0200	February
TC-43	12	1	15	—	20	1945-0226	May
CHG-89	5	1	15	—	120-240	2058-2332	July
TC-46	45	2	14	—	50	1934-0234	October
HMS-47	51	1	10	—	576	2013-2158	November
Enoploteuthis jonesi							
TC-7	12	1	82	F	9-13	1926-2056	August
TC-7	12	1	47	M	9-13	1926-2056	August
TC-32	28	1	40	F	92-122	1952-0152	July
CHG-89	24	1	35	M	90-130	2053-2246	February
TC-32	46	1	35	F	77-118	1951-0151	August
TC-32	39	1	30	F	63-101	1053-0153	August
CHG-89	14	1	27	M	70-80	0258-0445	February
CHG-89	29	1	22	—	120-135	2038-2231	February
CHG-89	31	1	17	—	90-150	2040-2233	February
TC-32	37	1	11	—	55-123	0354-0954	August
Enoploteuthis higginsi							
TC-32	28	1	60+	F	8-60	1952-0152	July
TC-32	22	1	53	F	67-117	1952-0152	July
TC-32	45	1	47	F	12-31	1143-1743	August
TC-32	41	1	46	M	59-122	1151-1751	August
TC-32	23	1	46	M	17-25	0403-1003	July
TC-32	56	1	45	F	97-179	1952-0152	August
TC-32	38	2	37-40	F	8-25	1144-1744	August
TC-32	44	1	37	F	72-118	0353-0953	August
Teritu	6	1	37	M	110	—	September
TC-32	48	1	35	F	60-104	1155-1755	August
CHG-89	11	1	35	M	100-200	0254-0445	February
TC-32	37	1	32	F	55-123	0354-0954	August
TC-32	38	1	30	M	8-25	1144-1744	August
TC-32	33	1	30	F	83-99	1950-0150	August
TC-32	56	1	29	F	97-179	1952-0152	August
TC-32	46	2	27-28	—	77-118	1951-0151	August
HMS-47	51	1	27	—	576	2013-2153	November
TC-32	37	1	22	—	55-123	0354-0954	August
TC-32	33	2	12-19	—	83-99	1950-0150	August
CHG-89	29	1	16	—	120-135	2038-2231	February
CHG-51	164	1	12	—	0-100	2105-2323	February

TABLE 6.—*Continued.*

Cruise no.	Station no.	No. of specimens	Mantle length (mm)	Sex	Depth (m)	Time 24 h	Month
CHG-51	172	1	12	—	0-100	2100-2250	February
CHG-89	30	1	11	—	100-125	0603-0745	February
Enoploteuthis reticulata							
CHG-7		[2]1	130	M	—	daylight	February
HMS-30	3	1	117	M	100	2105-2315	July
TC-32	31	1	71	M	30-121	0354-0954	August
TC-32	15	1	62	F	16-30	0352-0952	July
TC-32	48	1	50	M	60-104	1155-1755	August
TC-32	29	1	46	M	8-60	0343-0755	July
TC-32	9	1	45	F	17-25	0354-0954	July
TC-32	15	1	39	F	16-30	0352-0952	July
TC-32	3	1	35	F	12-15	0355-0955	July
TC-32	46	1	32	—	77-118	1951-0151	August
TC-32	28	1	30	—	92-122	1952-0152	July
TC-7	5	1	26	—	60-100	2023-2156	August
TC-32	6	1	18	—	83-124	0354-0954	July
TC-32	4	1	13	—	75-107	1146-1747	July

[1] From stomach of *Alepisaurus*.

[2] Regurgitated by a porpoise.

condition of the specimen. *Enoploteuthis galaxias, chuni,* and *theragrae* have a midventral row of photophores on the head flanked by two lateral rows which extend (without branching) to the ventral arms. These three species are found in the western Pacific: *chuni* and *theragrae* from Japan and *galaxias* from Australia. The remaining species of this complex, *anapsis, jonesi,* and *higginsi,* are very similar: All have distal club sucker rings without teeth; all have an incomplete midventral row of photophores on the head (represented by a short anterior segment near the base of the ventral arms and by a triangular patch of photophores in the apex of the funnel groove); the first lateral row of photophores on the head is divided and reunited before extending to the ventral arms; and all have an incomplete photophore row on arm III. The longitudinal rows of photophores on the mantle are easily recognized in *anapsis* and *jonesi*, but not in *higginsi*.

Enoploteuthis leptura, octolineata, obliqua, and *reticulata* comprise the other species complex. They all have thin, slender, and short tentacles, clubs without semilunar membranes, few club suckers that lie in two rows, and a continuous midventral space on the head. *Enoploteuthis octolineata* and *E. leptura* are similar in that both have distinctly separated first and second lateral rows of photophores on the head, and lack a triangular patch of photophores in the apex of the funnel groove although each of the first lateral rows continues into the groove. Both species also have distinct and well-spaced mantle and funnel photophores. *Enoploteuthis reticulata* and *E. obliqua* also show similarities. The photophore pattern on the head, arms, and funnel have basically the same arrangement: Two small clusters of photophores, separated by a narrow space, are present in the apex of the funnel groove and, except for the continuous midventral space, single photophores are present posteriorly in the spaces between the funnel photophore rows. Thus, the rows are not completely separated. However, the mantle photophore pattern of each species is distinct: oblique in one and reticulate in the other. *Enoploteuthis reticulata* and *E. galaxias* have similar patterns of mantle photophores, but their head photophore patterns and some features of the clubs differ. The reticulate pattern on the mantle is probably an independently developed trait.

The spermatophores of *E. higginsi* and *E. anapsis* are both intricately sculptured, while those of *E. leptura, E. obliqua,* and *E. reticulata* are simple. Since the spermatophores of the other species are undescribed, it remains to be seen if the sculptured type are only associated with the first species complex and the simple type with the second complex. The important characters (except photophore pattern) of these two complexes are listed in Table 7.

KEY TO THE SPECIES OF *ENOPLOTEUTHIS* (ADULTS, WORLDWIDE)

1. Tentacular stalk and club narrow, suckers on dactylus few and in two rows; carpal cluster elongate; semilunar membrane absent 2

TABLE 7.—Some comparative features of *Enoploteuthis anapsis* and *E. leptura* complexes. ML = mantle length.

Species	Maximum ML (mm)		Tentacle length index	Club length index	Carpal suckers	Shape of carpus	Club hooks No.	Club suckers No.	Club suckers arrangement	Club sucker ring teeth No.	Semi-lunar membrane
	Female	Male									
anapsis complex											
chuni	87	63	119.0-147.0	21.6-25.4	4-6	polygonal, oval	9	90	quadriserial	5-8	present
galaxias	87	73	102.6-108.3	25.6-26.4	4-6	round, oval	11	38-43	quadriserial	undescribed	absent
theragrae	80	60	83.3-91.3	25.0	5	ellipsoid	10	many, minute	quadriserial	undescribed	absent
anapsis	76.9	54	163.0-275.7	29.1-47.1	3-4	rectangular	12-13	40-50	quadriserial	absent	present
jonesi	82	47	104.9-188.9	24.4-40.7	3-4	round	13-14	60-72	quadriserial	absent	present
higginsi	60+	46	110.8-239.1	29.7-36.1	2-3	oval	10-12	60-72	quadriserial	absent	present
leptura complex											
leptura	44.5	79	89.0-96.0	17.9-20.6	5-6	elongate	6-12	10-15	biserial	7	absent
obliqua	50	58	62.1-96.4	17.0-26.0	4-5	elongate	8-9	11-17	biserial	6-7	absent
reticulata	62	130	79.5-129.0	15.4-30.4	4-7	elongate	8-12	8-11	biserial	6-7	absent
octolineata	75	46	93.3-112.7	25.0-28.3	3-6	elongate	9-11	16-17	biserial	10	absent

1. Tentacular stalk and club robust, suckers on dactylus many and in four rows; carpal cluster round to oval; semilunar membrane present or absent 5

2. Mantle photophores in longitudinal rows only 3
2. Mantle photophores in longitudinal and/or oblique rows 4

3. Eight well-spaced mantle rows, all reaching anterior mantle edge; eight photophore rows on head, second and third lateral rows united posteriorly .... *octolineata*
3. Seven well-spaced mantle photophore rows, only six reaching anterior mantle edge; eight photophore rows on head, none united .... *leptura*

4. Two photophore rows on median part of mantle, oblique photophore rows on sides .... *obliqua*
4. Longitudinal rows and intersecting oblique rows of photophores on mantle (reticulate pattern) .... *reticulata*

5. Midventral photophore rows on head complete; first and second lateral photophore rows unbranched; photophore row on arm III complete 6
5. Midventral photophore row on head incomplete; first lateral photophore row on head divided and reunited; photophore row on arm III incomplete 8

6. Eight photophore rows on mantle, distinct for one-third of mantle length; semilunar club membrane present .... *chuni*
6. Six photophore rows on mantle or no rows, photophores scattered; semilunar club membrane absent 7

7. Six photophore rows on mantle, photophores scattered on posterior half of mantle......................... *theragrae*
7. No photophore rows on mantle, mantle photophores scattered; some areas devoid of photophores .... *galaxias*

8. Mantle photophores not in rows, photophores scattered .... *higginsi*
8. Six longitudinal photophore rows separated by narrow space................ 9

9. Midventral space not extending to tail, this space occupied by scattered photophores near tail .... *anapsis*
9. Midventral mantle space narrow, extending to tail...................... *jonesi*

ACKNOWLEDGMENTS

I am indebted to J. C. Marr and B. J. Rothschild, past directors, and R. S. Shomura, present director, Honolulu Laboratory of the National Marine Fisheries Service (formerly the Biologcal Laboratory of the Bureau of Commercial Fisheries) at Honolulu, Hawaii, for extending me the use of the facilities of the laboratory, library, and office space during my extended stay in Honolulu. I thank Hazel S. Nishimura, Librarian, for her help and patience in locating cephalopod literature. I also appreciate the hospitality and assistance of the scientific and clerical staff of the laboratory. I give special thanks to E. C. Jones for his efforts to retrieve all the squid material collected in net tows made on the various cruises of the vessels operated by the Honolulu Laboratory between 1967 and 1970 and for ensuring that the material reached me in good condition.

I extend my deepest gratitude to C. F. E. Roper of the Mollusk Division of the U.S. National Museum of Natural History, Washington, D.C., and R. E. Young of the Department of Oceanography, University of Hawaii, Honolulu, Hawaii, both of whom unselfishly gave much attention and expert advice on the systematics of squids and on the preparation of this paper; and to G. L. Voss of the Rosenstiel School of Marine and Atmospheric Science, Miami, Fla., who initially suggested the investigation of the Pacific cephalopod material at the Honolulu Laboratory and who reviewed the manuscript prior to publication—his constructive criticism is greatly appreciated. R. E. Young donated the holotype of *Enoploteuthis higginsi*.

Finally, I sincerely thank T. Okutani of the National Science Museum (Natural History Institute), Tokyo, Japan, and M. Okiyama, University of Tokyo, for examining *E. chuni* specimens and offering their opinions and observations on Japanese *Enoploteuthis*; and W. F. Ponder of the Australian Museum, Sydney, Australia, for allowing me to examine the holotype of *E. galaxias* during my visit to that museum.

LITERATURE CITED

ADAM, W.
1960. Cephalopoda from the Gulf of Aqaba. Sea Fish. Res. Stn., Haifa, Bull. 26:1-26.
1973. Cephalopoda from the Red Sea. Bull.Sea Fish. Res. Stn., Israel, 60:9-47.

BERRY, S. S.
1911. Note on a new *Abraliopsis* from Japan (*A. scintillans*, n. sp.). Nautilus 25:93-94.
1914. The Cephalopoda of the Hawaiian Islands. U.S. Bur. Fish., Bull. 32:255-362.
1918. Report on the Cephalopoda obtained by the F.I.S. "Endeavor" in the Great Australian Bight and other southern Australian localities. Biol. Results Fish. Exper. "Endeavor," 1909-1914, 4:203-298.

HOYLE, W. E.
1910. A list of the generic names of dibranchiate Cephalopoda with their type species. Abh. Senckenb. Naturforsch. Ges. 32:407-413.

ISHIKAWA, C.
1914. Uber eine neue Art von Enoploteuthis, *Enoploteuthis chunii* spec. nov., aus Uwodu, Japanische Meer. J. Coll. Agric. Univ. Tokyo 4:401-413.

KING, J. E., AND I. I. IKEHARA.
1956. Comparative study of food of bigeye and yellowfin tuna in the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 57:61-85.

LEACH, W.
1817. Synopsis of the orders, families, and genera of the class Cephalopoda. Zool. Misc. 3:137-141.

NIXON, M., AND P. N. DILLY.
1977. Sucker surfaces and prey capture. *In* M. Nixon and J. B. Messenger (editors), The biology of cephalopods, p. 447-551. Symp. Zool. Soc. Lond., no. 38., Acad. Press, Lond.

OKUTANI, T.
1967. Preliminary catalogue of the decapodan mollusca from Japanese waters. Bull. Tokai Reg. Fish. Res. Lab. 50:1-16.
1968. Studies on early life history of decapodan mollusca.—III. Systematics and distribution of larvae of decapod cephalopods collected from the sea surface on the Pacific coast of Japan, 1960-1965. Bull. Tokai Reg. Fish. Res. Lab. 55:9-57.
1974. Epipelagic decapod cephalopods collected by micronekton tows during the EASTROPAC Expeditions, 1967-1968 (systematic part). Bull. Tokai Reg. Fish. Res. Lab. 80:29-118.

PFEFFER, G.
1900. Synopsis der oegopsiden Cephalopoden. Mitt. Naturhist. Mus. Hamburg 17:145-198.

RANCUREL, P.
1970. Les contenus stomacaux d'*Alepisaurus ferox* dans le sud-ouest Pacifique (Céphalopodes). [In Fr., Engl. summ.] Cah. O.R.S.T.O.M., Ser. Oceanogr. 8(4):3-87.

REINTJES, W. J., AND J. E. KING.
1953. Food of yellowfin tuna in the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 54:91-110.

ROPER, C. F. E.
1964. *Enoploteuthis anapsis*, a new species of enoploteuthid squid (Cephalopoda, Oegopsida) from the Atlantic Ocean. Bull. Mar. Sci. Gulf Caribb. 14:140-148.
1966. A study of the genus *Enoploteuthis* (Cephalopoda: Oegopsida) in the Atlantic Ocean with a redescription of the type series, *E. leptura* (Leach, 1817). Dana Rep.

Carlsberg Found. 66, 46 p.

1977. Comparative captures of pelagic cephalopods by midwater trawls. Symp. Zool. Soc. Lond. 38:61-67.

ROPER, C. F. E., AND R. E. YOUNG.

1975. Vertical distribution of pelagic cephalopods. Smithson. Contrib. Zool. 209, 51 p.

SASAKI, M.

1914. Observations on Hotaru-ika *Watasenia scintillans*. J. Coll. Agric. Tohoku Imp. Univ. 6:75-107.

1920. Report on the cephalopods collected during 1906 by the United States Bureau of Fisheries steamer "Albatross" in the northwestern Pacific. Proc. U.S. Natl. Mus. 57:163-203.

SHIMOMURA, T., AND H. FUKATAKI.

1957. On the year round occurrence and ecology of eggs and larvae of the principal fishes in the Japan Sea—I. Bull. Jpn. Sea Reg. Fish. Res. Lab. 6:155-290.

TAKI, I.

1964. On eleven new species of the Cephalopoda from Japan, including two new genera of Octopodinae. J. Fac. Fish. Anim. Husb., Hiroshima Univ. 5:277-330.

YOUNG, R. E.

1978. Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. Fish. Bull., U.S. 76:583-615.

LIFE HISTORY STUDIES OF THE SANDWORM, *NEREIS VIRENS* SARS, IN THE SHEEPSCOT ESTUARY, MAINE

EDWIN P. CREASER AND DAVID A. CLIFFORD[1]

ABSTRACT

Little information is available on the life history of the sandworm, *Nereis virens*, in Maine despite their commercial importance over more than 40 years. Life history studies were performed in a flat along the Sheepscot River at Wiscasset, Maine, which was closed to commercial digging. Salinity varied between 17 and 29‰ at the surface and between 24 and 29‰ on the bottom, and temperature varied between −1° and 15°C at the surface and −1° and 14°C on the bottom. The proportions of potential male and female spawners changed with size; for worms <30 cm, the proportions were equal whereas a preponderance of females existed for worms >30 cm. Thirty percent of the largest worms displayed no sign of sexual development. Single eggs of 50 μ diameter were first observed in the coelom from October to November. These eggs entered a rapid growth phase between August and December and attained a maximum diameter of from 183 μ (1967) to 194 μ (1968) at time of spawning during April and May. Maturation could take as long as 18-20 months or as little as 12 months. The numbers of eggs laid by sandworms were found to vary between 0.05 (16 cm worm) and 1.3 million eggs (54 cm worm). The onset of spawning occurred when the surface water temperature was between 7.0°C (1968) and 8.1°C (1967) and when the bottom water temperature was between 6.7°C (1968) and 7.6°C (1967). During both years, spawning occurred 4 days after full moon during the period of spring tides. Scuba observations revealed that male spawners emerged from the mud about 3 hours after high water. At the peak of spawning, densities of epitokes may reach 1 worm/m^2. Male spawners are readily consumed by herring gulls, *Larus argentatus*.

The sandworm, *Nereis virens* Sars, commonly occurs on the Atlantic coast from Virginia northward to the Arctic region. It is also found in Iceland, Norway, Ireland, and the North Sea to France (Pettibone 1963).

Nereis virens is known to inhabit coarse and fine muddy sand, mussel beds, and the roots of decaying marsh and eelgrass (Pettibone 1963). The sandworm population in the Sheepscot River study area at Wiscasset, Maine (lat. 44°N, long. 70°40′W), inhabits a gray, silty clay which is moderately burrowed and contains shell fragments, mica flakes, and 2% organic carbon (Reynolds et al. 1975[2]). The mean tidal amplitude in this region is 2.9 m.

Ecologically, sandworms occupy an important position in the food web of other invertebrates, fish, and shorebirds. They have been harvested commercially for bait along the Maine coast for more than 40 years, with landings of 26.9-38.1 million worms/yr and a landed value of $0.5-1.1 million reported between 1966 and 1980 (NMFS 1966-80).

Previous research on Maine sandworms included studies on digging (Ganaros 1951[3]) and dispersion (Gustafson 1953; Dean 1978). Although intensive harvesting qualifies the sandworm for management considerations, only reports by Glidden (1951)[4] and Dow and Creaser (1970) contain life history information pertinent to management of sandworm populations in Maine. The present study was undertaken to provide life history information for a sandworm population in the Sheepscot Estuary at Wiscasset, Maine. It also includes some information on subjects not previously investigated or which differ from findings reported from other geographical locations.

Other studies on the life history and reproduction of *Nereis virens* include Brafield and Chapman (1967) and Bass and Brafield (1972) in the Thames Estuary at Southend, England; Sveshnikov (1955) in Rugozerski Bay near the White Sea,

---

[1] Maine Department of Marine Resources Research Laboratory, West Boothbay Harbor, ME 04575.

[2] Reynolds, L., J. Bowman, and E. Kelly. 1975. Unpublished summary of sediment size, x-radiography, chemistry, and mass physical properties of six cores and two grabs from Maine. U.S. Naval Oceanographic Office, Washington, D.C.

[3] Ganaros, A. 1951. Commercial worm digging. Bull. Dep. Sea Shore Fish., Augusta, Maine, 6 p.

[4] Glidden, P. E. 1951. Three commercially important polychaete marine worms from Maine. Rep. Dep. Sea Shore Fish., Augusta, Maine, 25 p.

Manuscript accepted April 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

Russia; and Snow and Marsden (1974) at Brandy Cove, St. Andrews, New Brunswick, Canada.

Materials and Methods

All sandworms were collected in the vicinity of a small intertidal mud flat at Wiscasset, Maine, closed to commercial digging. Within this area, a section running parallel to the low-water mark and measuring 91 m × 24 m was used for experimental purposes. Differences in tidal height between the upper and lower extremities of this experimental area were about 22 cm. Monthly, three 1 m^2 sample plots were randomly chosen and dug within the experimental site. The sampling device consisted of a 1 m^2 frame with deep walls (45 cm) that could be pushed into the mud to prevent escape. Within each plot, the surface ooze was removed with a dustpan to a depth of 2-3 cm and deposited within a square framed receptacle constructed of 1 mm mesh fiberglass screen. The receptacle was then partially immersed in the river and carefully agitated to remove sediment. The remaining debris and worms were poured into a plastic container and transported to the laboratory. Small portions of debris, together with seawater, were deposited in dissecting trays and dispersed with a needle probe. The contents were thoroughly searched and all small sandworms, swimming or hiding among the debris, were removed with forceps. Clumps of deeper and firmer mud were removed from the sampling device in the field to the maximum depth of burrowing activity (about 30 cm) and carefully broken by hand to remove the larger worms intact. These worms were also transported to the laboratory in plastic buckets.

All sandworms were acclimated to high salinity water (about 32‰) at the laboratory prior to immersion in anesthetic (7.5% $MgCl_2$). Lengths were obtained using a V-shaped measuring trough containing ample anesthetic to cover the worms. Coelomic fluid was withdrawn with the aid of capillary pipettes, and sex was determined by microscopic examination of the contents. Egg diameters were measured with an ocular micrometer and without a cover slip. Usually 10 eggs were measured from each worm. The relationship of sandworm length to numbers of eggs laid was corrected for transformation bias following the methodology of Bradu and Mundlak (1970).

Worms used in the study to determine the percent of mature males and females and immature females in each length increment were obtained during February (prior to spawning) from pooled samples dug independently of the regular monthly sample. The distinction between mature and immature females was made after examining eggs in the coelomic fluid; large eggs from mature worms would be spawned in April or May, and small eggs would be spawned approximately 1 yr later. We were unable to make a distinction between mature and immature males.

Sandworms designated "nonspawners" include worms of all sizes that have not spawned and whose coelomic contents present no clue about sexuality. "Spent" worms include both males and females that have spawned and are deteriorating and approaching death.

Female sandworms used for egg counts were anesthetized, measured, and preserved. The worms were then split lengthwise and washed thoroughly to remove as many eggs as possible. Next, the body was chopped into 1 cm pieces, immersed in seawater, and stirred magnetically. After three or four changes of water, most eggs were dislodged. Egg samples were diluted in 0.1-2.7 l seawater, depending upon size of the worm and numbers of eggs present. Two 1 ml aliquots were withdrawn from this mixture during agitation, placed on Sedgwick-Rafter[5] counting cells, and the number of eggs counted under the 10× objective. The mean value was then multi-

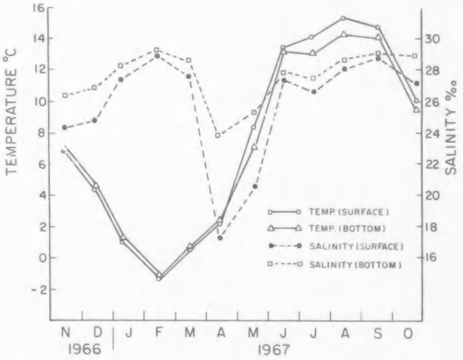


FIGURE 1.—Summary of temperature and salinity data collected from the Sheepscot River near the Wiscasset closed area between November 1966 and October 1967.

---

[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

plied by the dilution factor to obtain the final egg count.

Hydrographic data were usually obtained shortly after the collection of worm samples. Mean monthly water temperature was calculated from 25 thermister recordings collected in situ at 30-min intervals at hydrographic stations occupied for 12 h. Mud temperature records were collected in situ by digging a shallow hole in the mud flat and inserting a thermometer horizontally at a depth of about 10 cm. Water samples used in salinity analysis were obtained using a 1 l water sampler. Water samples of 5 ml were analyzed for salinity by the Knudsen method.

Sandworms were captured during spawning using scuba techniques or dip nets.

RESULTS

Salinity and Temperature of the Study Area

The salinity and temperature regime of the river water at the study area during the period November 1966-October 1967 is summarized in Figure 1. During these studies, surface salinity varied between 17 and 29‰, surface temperature between −1° and 15°C, bottom salinity between 24 and 29‰, and bottom temperature between −1° and 14°C.

Length Frequency

Preliminary digging in the Wiscasset closed area indicated that sandworms were most abundant in the region of the low-water mark. Within this region, significant variations in both abundance and size were recorded for three randomly selected 1 m^2 plots dug from one tidal height during one time period. Because of this variation, digging more than 1 sample plot/mo was desirable. We elected to dig and combine the results of 3 randomly selected plots/mo because the combined results produced fairly consistent length-frequency trends between months. Considerable breakage of all sizes of sandworms was encountered during handling and processing. During agitation, the presence of sharp shells and debris in the upper layer of organic ooze resulted in additional breakage of juvenile sandworms prevalent there. Some unavoidable bias has therefore resulted in the numbers of juvenile worms reported. Length-frequency results for all whole worms collected during August, September, and October are shown in Figure 2. Sandworms captured varied in length between <1 and 31 cm. Numbers of whole individuals captured during these months varied between 546 and 701. Figure 2 indicates some recruitment of small individuals into the sampled population during the summer. Additional length-frequency information collected during this study is presented in Creaser and Clifford (1981)[6].

The August-October 1967 length-frequency data, when combined to produce sufficient number, was analyzed by the method of Harding (1949), as explained by Cassie (1950), to determine the number of assumed age modes. Although five assumed modes and linear growth were detected by this analysis, there is considerable overlap in length at age; the results are therefore questionable until they can be verified against other aging techniques.

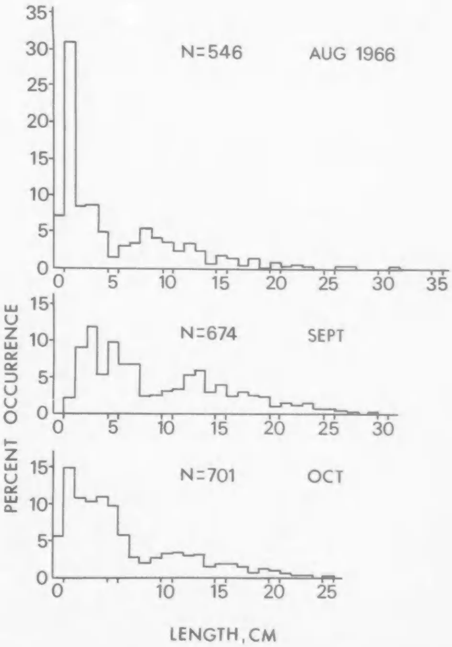


FIGURE 2.—Monthly length frequency distributions for three combined plots dug from the Wiscasset closed area.

---

[6] Creaser, E. P., and D. A. Clifford. 1981. Life history studies of the sandworm *Nereis virens* Sars, in the Sheepscot Estuary, Maine. Maine Department Marine Resources Research Laboratory, Res. Ref. Doc. 81/16, 37 p.

Proportions of male, female, and nonspawning sandworms of various lengths are shown in Figure 3. There is an increase in numbers of mature males and females with increasing size. Worms >30 cm show a preponderance of mature females over mature males. More than 30% of the largest worms showed no sign of sexual development.

Oocyte Development

The results of oocyte growth studies are presented in Figure 4A, and water temperatures associated with these data are shown in Figure 4B. Eggs of about 50 μ were first observed in the coelom in October-November. Diameter increased from 80 to 160 μ during the rapid-growth phase which occurred between August and December. Prior to spawning, the rate of egg growth decreased. Maximum mean egg diameters obtained were 183 μ (1967) and 194 μ (1968). A Student's *t*-test revealed a significant difference between these mean diameters ($t = 4.65910$; $P<0.05$; 14 df). Spawning occurred in April and May during a 4-5 wk period, and few egg-bearing worms were found after the beginning of June. The maturation of gametes required 18-20 mo, or as little as 12 mo, depending upon when the eggs were ovulated into the coelom. Annual spawning, together with a maximum development period of 18-20 mo, accounted for the presence of two general egg sizes in sandworms inspected between October-November and April-May. Eggs approaching spawning size varied the least in diameter (the smallest standard deviation) (see Figure 4A). During the period of rapid egg growth, both mud and bottom river temperatures were decreasing (see Figure 4B).

Numbers of Eggs Laid

The numbers of eggs laid by sandworms of various lengths are recorded in Figure 5. The range varies between about 0.05 and 1.3 million eggs for worm lengths of 16 and 54 cm, respectively.

Environmental Conditions During Spawning

Spawning first occurred in the Wiscasset region on 28 April 1967 and 17 April 1968. A summary of hydrographic conditions associated with spawning on 2 May 1967 and 19 April 1968 is presented in Table 1. Table 1 shows that mean surface-water temperatures of 7.0°C (1968) and 8.1°C (1967) and bottom water temperatures of 6.7°C (1968) and 7.6°C (1967) were associated with the onset of spawning. During both years, initial activity in the Wiscasset area occurred 4 d after full moon during the period of spring tides. The stage of the tide during which spawning activity occurs was investigated on 23 April 1968, using scuba techniques. During a series of six dives beginning just after high water (08:28

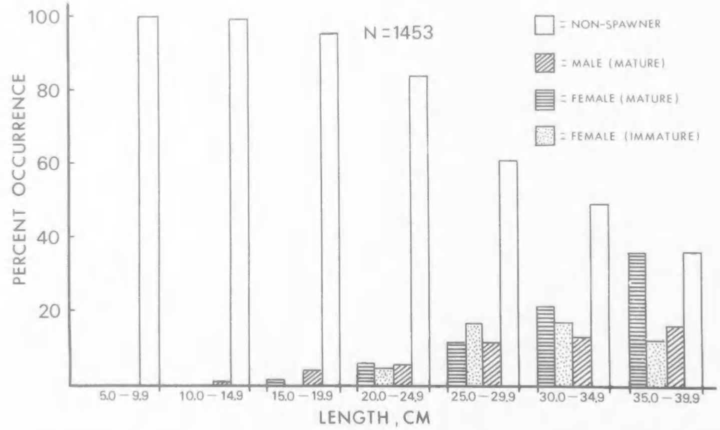


FIGURE 3.—Proportions of male, female, and nonspawning sandworms of various lengths collected prior to spawning during February 1967.

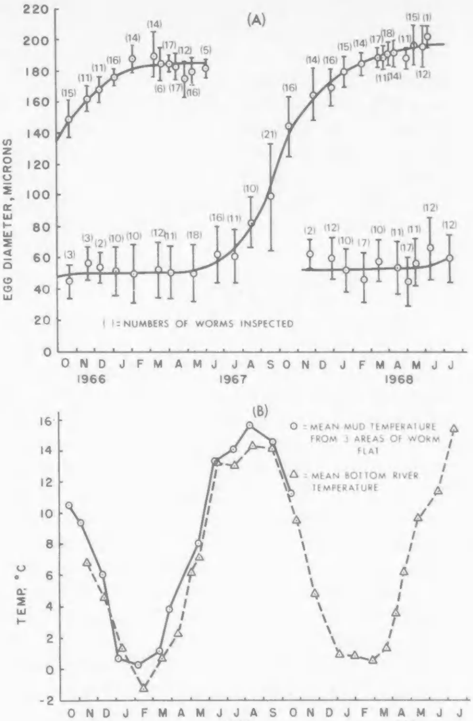


FIGURE 4.—(A) Oocyte growth occurring simultaneously in two groups of Wiscasset sandworms at different stages of maturation (lines fitted by eye). (B) Monthly mean mud and bottom water temperature from the Sheepscot River at Wiscasset.

TABLE 1.—Summary of temperature and salinity associated with sandworms spawning at Wiscasset, Maine, on 2 May 1967 and 19 April 1968.

	2 May 1967 1030-1430 h			19 April 1968 0730-1200 h		
	Temp. (°C)	Salinity (‰)	*N*	Temp. (°C)	Salinity (‰)	*N*
Surface						
$\bar{x} \pm 1$ SE	8.1±0.3	19.98± 0.38	9	7.0±0.2	23.55± 0.25	10
Range	6.8–9.1	18.51–21.58	9	5.8–7.8	22.75–25.08	10
Bottom						
$\bar{x} \pm 1$ SE	7.6±0.2	23.18± 0.43	9	6.7±0.2	25.34± 0.26	10
Range	6.6–8.4	21.24–25.32	9	5.3–8.0	23.80–26.09	10

EST) and ending just before low water (14:34 EST), no spawning worms were observed until about 3 h after high water (Table 2). Although the possible role of water temperature in initiating spawning cannot be completely eliminated, the tidal-condition results in Table 2 are consistent with numerous visual observations on spawning activity in the Wiscasset area over many years.

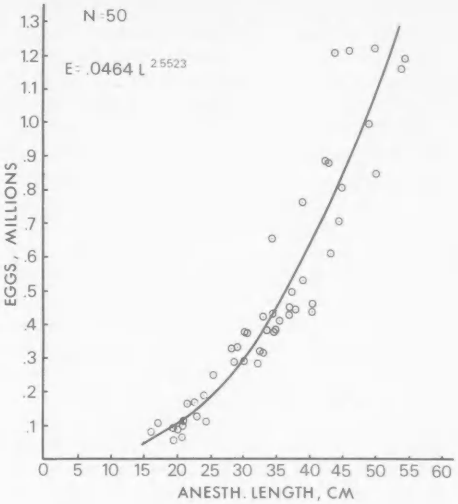


FIGURE 5.—Number of eggs produced as a function of sandworm length.

Spawning Characteristics

Nearly all sandworms captured during spawning were males. Females were only rarely encountered in the latter part of the spawning season. Scuba observations revealed that male sandworms emerge from the mud anterior-end

TABLE 2.—Data collected during scuba investigation of tidal conditions between high water and low water at onset of spawning activity on 23 April 1968.

Time of dive	Tide height (m)	Temperature (°C)		Salinity (‰)		No. worms collected	
		Surface	Bottom	Surface	Bottom	♂	♀
(High water 0828 h EST)							
0910-0930	3.4	7.3	6.1	24.24	26.64	0	0
1010-1028	2.9	7.6	6.5	25.12	26.24	0	0
1103-1123	2.1	8.1	7.7	24.87	24.74	0	0
1200-1222	1.2	8.8	8.2	24.61	24.69	127	0
1305-1335	0.6	9.4	9.1	25.16	25.26	118	0
1400-1410	0.5	11.2	10.4	24.72	24.98	96	0
(Low water 1434 h EST)							

first. These free-swimming spawners displayed two characteristic types of swimming behavior: 1) Swimming more or less in a straight path (with occasional tumbling and back swimming) with typical lateral undulations of the body, and 2) swimming in circles typically 10-15 cm in diameter. Spawning worms appeared to be distributed randomly over the flats. During peak spawning, the density of worms observed swimming near the surface of the mud was about 1 worm/m^2. All male spawners collected in the Wiscasset area were definitely epitokous individuals, having undergone morphological changes. Mature female sandworms dug from the flats were typically dark green, males that had just emerged to spawn were lighter green, and males that were "spawned out" but still swimming were a dark, bluish green. Some male sandworms may spawn during more than one tide. Numerous male sandworms were observed burrowing back into the flats during scuba dives. None, however, burrowed deeply into the mud. The reproductive strategy of the sandworm qualifies it as a "monotelic" species, i.e., it breeds once in its lifetime, all gametes are released in one or two large batches, and the spent animals die immediately or shortly afterwards without developing more gametes (Clark cited in Stancyk 1979). Some nearly "spent" individuals were observed to contain large numbers of a parameciumlike ciliate.

Predation

During receding tides in the Wiscasset vicinity during April, an increasing number of herring gulls, *Larus argentatus* Pontoppidan, circling the flats, anticipated the ensuing spawning activity of *Nereis virens*. At the height of spawning, thousands of gulls could be observed feeding on male spawners.

DISCUSSION AND CONCLUSIONS

Salinity and Temperature of the Sandworm Habitat

The salinity and temperature regime encountered by *Nereis virens* in other geographical areas is incomplete. Brafield (1968)[7] indicated that water and interstitial salinity encountered by the Southend, England, sandworm population varied between 28-32‰ and 27.5-31.5‰, and water temperature varied between 3.2°C (January) and 22.5°C (August). The Wiscasset population is subjected to more estuarine salinity conditions and cooler water temperatures than in England. The temperatures recorded for Brandy Cove, New Brunswick, by Snow (1972) are very similar to the temperatures recorded in Figures 1 and 4B.

Length-Related Observations

The concave nature of the length-frequency data presented in Figure 2 is consistent with a highly variable recruitment pattern resulting from larval mortality and intense predation soon after settlement (Warwick cited in Coull 1979).

The absence of sexual products in the coelom of a proportion of the largest sandworms (see Fig. 3) appears to be characteristic of the species. Both Snow and Marsden (1974) and Brafield and Chapman (1967) have made similar observations. The fate of these large nonspawners is not known. They possibly emigrate to subtidal or downriver habitats or succumb to natural or digging mortality without spawning.

Considerable variation exists in the maximum size of *Nereis virens* reported from different geographical locations. The largest individual reported in Figure 2 was 31 cm. Sandworms of 70-75 cm (anesthetized length) have been dug from the Back River in Boothbay, Maine (lat. 43°54′15″ N, long. 69°40′ W). Sveshnikov (1965) reported catching epitokous individuals 45 cm in length and also reported that the heteronereid form of *N. virens* reached a length of 90 cm along the coast of England and 1 m in Japan. Khlebovich (1963) reported mature individuals reaching 38.5 cm in the White Sea.

The sex ratio of *Nereis virens* collected prior to spawning varies with geographical location. In our studies, the sex ratio of small potential spawners was approximately 1 female:1 male, whereas the sex ratio of individuals ≥30 cm was approximately 2 females:1 male. There is no reason to believe that these changes in sex ratios with size result from nonspawners (in February) becoming sexually mature by spawning onset in April. Our observations reveal that the maturation rate of both eggs (see Figure 4A) and sperm requires considerably more than 2 mo. The change in sex ratio may indicate that larger potential males are more disposed to either free-swimming in the water or exposing themselves on the surface of the mud, and are therefore subject to greater natural mortality through predation. The free-swimming habits of *Nereis virens* (especially at night) have been well documented (Crowder 1923; Gustafson 1953; Dean 1978). Brafield and Chapman (1967) reported that by the onset of spawning, males and females occurred in about equal numbers. Snow (1972), on the other hand, reports a 3:1 ratio of males to females prior to spawning.

---

[7] A. E. Brafield, Department of Biology, Queen Elizabeth College (University of London), Campden Hill Road, London, England, pers. commun. 1968.

Oocyte Development

Some similarities exist between our studies of oocyte development (see Figure 4A) and those of Brafield and Chapman (1967) and Snow and Marsden (1974). Brafield and Chapman (1967) reported that ovulation occurred in February or March at 50 μ and the oocyte diameters increased from 80 μ to 160 μ during the period of rapid growth between September and December. The increase in oocyte diameters to 170-180 μ prior to spawning required about 14 mo. Snow (1972) reported that the smallest eggs found free in the coelom of *Nereis virens* measured 10 μ in diameter. The eggs usually remained in clumps until they measured 25 μ and appeared singly above 50 μ. Snow and Marsden (1974) stated that the rapid-growth phase began in September, and their egg growth figure showed that this extended at least until December. They stated that maturation required 1-2 yr, depending upon the time of year when the eggs were produced. Ova measured 210-240 μ when spawned in May.

The standard deviation for oocyte diameters recorded in both the present study and that of Brafield and Chapman (1967) reveals that small oocytes are more variable in size than large oocytes. The large standard deviation for small oocytes results from ovulation occurring over a long period. Eventually, the maturation rate of oocytes produced late in this period accelerates so that all oocytes mature at a certain size at the same time (Clark cited in Stancyk 1979). Similar observations have been recorded for *Nereis diversicolor* Müller (Clark and Ruston 1963).

Oocyte development in *Nereis virens* follows the typical sigmoid growth curve. Similar observations have been recorded for all or part of the oocyte maturation processes in *Arenicola marina* Linnaeus (Howie 1964 pers. commun. cited in Clark 1965), *Nereis diversicolor* (Clark and Ruston 1963), and *Glycera dibranchiata* Ehlers (Creaser 1973).

Although no length measurements were obtained for the sandworms used in Figure 4A, it was generally evident to us that no relationship existed between size of the adult and size of the eggs; potential spawners of all sizes at one time possessed eggs of similar size.

Numbers of Eggs Laid

Sandworms >37 cm long were not found in the Wiscasset closed area (Creaser and Clifford footnote 6). However, a few larger worms, up to 54 cm long, were captured adjacent to the closed area after extensive digging, and egg counts from these as well as the more typical sizes were included in this study. Sandworms contained considerably fewer eggs than were found in similar-sized bloodworms, *Glycera dibranchiata*, collected from the same closed area but higher on the flat (Creaser 1973). The relatively large numbers of eggs produced (0.05-1.3 million), however, are consistent with the observation that macrofauna species generally produce large numbers of gametes (Thorson 1950 cited in Coull 1979).

Environmental Conditions During Spawning

Clark and Olive (1973) reported that "In the family Nereidae, sexual maturation and epitoky are caused by a decline in the rate of production of a cerebral hormone." Clark (1965) suggested that changes in the secretion rate of cerebral hormone might be controlled by environmental conditions or by some feedback mechanism. A distinction is made between (a) necessary environmental conditions and (b) specific environmental signals (Clark cited in Stancyk 1979).

Results of the present study suggest that a water temperature of about 7°-8°C might be one of the necessary environmental conditions required to initiate spawning. This hypothesis is strengthened by the fact that Snow and Marsden (1974) successfully fertilized *Nereis virens* ova and reared the young in the laboratory at 7°C. Sveshnikov (1955) recorded that surface temperature varied between 8.9° and 9.5°C at time of spawning in the White Sea. Some investigators (Thorson 1946; Korringa 1957) have reported that a rise in seawater temperature triggers spawning in a number of marine organisms. Bass and Brafield (1972) induced premature spawning in *Nereis virens* with an artificial rise in temperature from ambient (5°C) to 22°C over a 10-h period.

The specific environmental signals required to initiate spawning may be associated with the phase of the moon and the stage of tide. Our observations of initial spawning activity shortly after full moon are in partial agreement with Pettibone (1963) who reported that the spawning activity of *Nereis virens* on the New England coast centered around both full and new moon. Brafield and Chapman (1967), Bass and Brafield (1972), and Snow and Marsden (1974) have reported that swarming coincided with the time of new moon. The sandworms at Wiscasset spawn during the second half of the outgoing tide through the first part of the incoming tide. Pettibone (1963) reported similar observations from Barnstable, Mass. Bass and Brafield (1972) reported swarming in the Thames population only during periods of day and night high tides. Our only observation of some exceptionally large *Nereis virens* swarming at high water occurred in the Damariscotta River, Maine, in the vicinity of Fort Island (lat. 43°53′30″ N, long. 69°31′30″ W).

Spawning Characteristics

Some of the characteristics of spawning *Nereis virens* recorded by different investigators are summarized in Table 3.

Nereis virens has been described as atokous (Brafield and Chapman 1967; Snow and Marsden 1974) and epitokous (Gustafson 1953; Sveshnikov 1955; Khlebovich 1963). Clark (1961) reported that the structural modification associated with epitoky may be subtle and consist only of an elongation of the setae, modification of the sense organs, and reconstruction of the musculature. According to this description, spawning individuals captured in the vicinity of Wiscasset were obviously epitokes; the same morphological changes recorded in England by Bass and Brafield (1972) for adult males were observed in the Wiscasset population. There is no reason to doubt that *Nereis virens* display different reproductive characteristics in different geographical locations. Dales (1950) reported that nereids are well known for displaying variable reproductive habits within a given species.

ACKNOWLEDGMENTS

We extend our appreciation to Clement Walton and Christy Adams for their assistance in the collection of data used in this research. Special thanks are also due to David Sampson for assistance in the analysis of data, James Rollins for

TABLE 3.—Some characteristics of spawning *Nereis virens* recorded by different investigators.

Investigators	Location of spawning males	Location of spawning females	Male swimming behavior during spawning	Color of spawners	Fate after spawning
Bass and Brafield (1972)	males in free-swimming swarms	believed females spawned in burrows	observed circular swimming in both vertical and horizontal plane; anterior portion of gravid worm becomes rigid.	4% of males deep red with white lines marking margin of anterior segments; a few were creamy white	worms swarmed several times before becoming spent but die after spawning
Brafield and Chapman (1967)	males in free-swimming swarms	believed females spawned in burrows or possibly spent short period swarming at surface		females lime green males milky green	worms die after spawning
Clark (1961)	males often dominate breeding swarms of nereids		swimming in tight circles is common to all swarming nereids		
Snow and Marsden (1974)	males in free-swimming swarms	believed females spawned in burrows			survival after spawning is highly unlikely
Our observations	males in free-swimming swarms	believed females spawned in burrows; some evidence that they emerge from mud to die after spawning	2 types: 1) swimming in straight lines is characteristic of new spawners that have just emerged from the mud; 2) circular swimming of spent or nearly spent individuals caused by anterior portion curved downward and worm tipped on side when swimming	females dark green males pale green becoming darker as worms become spawned out	individual worms sometimes spawn on more than one tide but die after spawning

photographic services, and Vicki Averill for typing.

This research was conducted by the Maine Department of Marine Rescurces Research Laboratory, West Boothbay Harbor, Maine, in cooperation with the United States Department of Commerce, National Marine Fisheries Service, and was financed under Public Law 88-309, Project 3-16-R.

LITERATURE CITED

BASS, N. R., AND A. E. BRAFIELD.
1972. The life-cycle of the polychaete *Nereis virens*. J. Mar. Biol. Assoc. U.K. 52:701-726.

BRADU, D., AND Y. MUNDLAK.
1970. Estimation in lognormal linear models. J. Am. Stat. Assoc. 65:198-211.

BRAFIELD, A. E., AND G. CHAPMAN.
1967. Gametogenesis and breeding in a natural population of *Nereis virens*. J. Mar. Biol. Assoc. U.K. 47:619-627.

CASSIE, R. M.
1950. The analysis of polymodal frequency distributions by the probability paper method. N.Z. Sci. Rev. 8:89-91.

CLARK, R. B.
1961. The origin and formation of the heteronereis. Biol. Rev. (Camb.) 36:199-236.
1965. Endocrinology and the reproductive biology of polychaetes. Oceanogr. Mar. Biol. Annu. Rev. 3:211-255.

CLARK, R. B., AND P. J. W. OLIVE.
1973. Recent advances in polychaete endocrinology and reproductive biology. Oceanogr. Mar. Biol. Annu. Rev. 11:175-222.

CLARK, R. B., AND R. J. C. RUSTON.
1963. The influence of brain extirpation on oogenesis in the polychaete *Nereis diversicolor*. Gen. Comp. Endocrinol. 3:529-541.

COULL, B. C.
1979. Marine benthic dynamics. Belle W. Baruch Library in Marine Science, No. 11. Univ. So. Carolina Press, Georgetown, S.C., 451 p.

CREASER, E. P., JR.
1973. Reproduction of the bloodworm (*Glycera dibranchiata*) in the Sheepscot estuary, Maine. J. Fish. Res. Board Can. 30:161-166.

CROWDER, W.
1923. Dwellers of the sea and shore. MacMillan Co., N.Y., 333 p.

DALES, R. P.
1950. The reproduction and larval development of *Nereis diversicolor*. O. F. Müller. J. Mar. Biol. Assoc. U.K. 29:321-360.

DEAN, D.
1978. Migration of the sandworm *Nereis virens* during winter nights. Mar. Biol. (Berl.) 45:165-173.

DOW, R. L., AND E. P. CREASER, JR.
1970. Marine bait worms, a valuable inshore resource. Atl. States Mar. Fish Comm. Leafl. 12, 4 p.

GUSTAFSON, A. H.
1953. Some observations on the dispersion of the marine worms *Nereis* and *Glycera*. Maine Dep. Sea Shore Fish. Fish Circ. 12.

HARDING, J. P.
1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141-153.

KHLEBOVICH, V. V.
1963. Biology of *Nereis virens* (Sars) in the Kandalakska Bay of the White Sea. Tr. Kandalakshkoga Gos. Zapov. 4:250-257.

KORRINGA, P.
1957. Lunar periodicity. Mem. Geol. Soc. Am. 67(1): 917-934.

NATIONAL MARINE FISHERIES SERVICE.
1966-1980. Monthly current fisheries statistics—Maine landings. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, Wash., D.C.

PETTIBONE, M. J.
1963. Marine polychaete worms of the New England region. I. Families *Aphroditidae* through *Trochochaetidae*. U.S. Natl. Mus., Bull. 227, 356 p.

SNOW, D. R.
1972. Some aspects of the life history of the Nereid worm *Nereis virens* (Sars) on an intertidal mud flat at Brandy Cove, St. Andrews, N.B. M.S. Thesis, McGill Univ., 161 p.

SNOW, D. R., AND J. R. MARSDEN.
1974. Life cycle, weight and possible age distribution in a population of *Nereis virens* (Sars) from New Brunswick. J. Nat . Hist. 8:513-527.

STANCYK, S. E.
1979. Reproductive ecology of marine invertebrates. Belle W. Baruch Library in Marine Science, No. 9. Univ. So. Carolina Press, Columbia, S.C., 283 p.

SVESHNIKOV, V. A.
1955. Reproduction and development of *Nereis virens* Sars. Dokl. ANSSSR Zool. 103:165-167.

THORSON, G.
1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Øresund). Medd. Dan. Fisk. Havunders. Ser. Plankton 4(1):1-523.

DIET OVERLAP BETWEEN ATLANTIC COD, *GADUS MORHUA*, SILVER HAKE, *MERLUCCIUS BILINEARIS*, AND FIFTEEN OTHER NORTHWEST ATLANTIC FINFISH

Richard W. Langton[1]

ABSTRACT

Diet overlap calculated as the percentage similarity between the diets of Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and 15 other finfish species was computed from stomach contents data collected in the northwest Atlantic between Cape Hatteras, North Carolina, U.S.A., and western Nova Scotia, Canada, from 1973 through 1976. Since crustaceans are preyed on by both Atlantic cod and silver hake and most of the 15 other groundfish species representing members of the Rajiformes, Perciformes, Gadiformes, and Pleuronectiformes, completely dissimilar diets occur very rarely. Although the overlap values are quite variable, the greatest overlap, with few exceptions, occurs among the gadiform fishes themselves rather than between the gadids and species from the three other ordinal taxonomic levels. Furthermore, Atlantic cod and silver hake show a size dependent shift in diet (at 60-70 cm for Atlantic cod and 20-25 cm for silver hake) from crustaceans to fish so that, generally, the major overlap levels are for the smaller size classes of fish. Overlap levels are discussed in relation to the prey species the predators share and also in terms of their usefulness in identifying potential trophic linkages between northwest Atlantic finfish.

The traditional way of identifying fish is by recognizing individual species as discrete taxonomic units. Although the species concept is fundamental to any biological work, fishery biologists have been considering other means of grouping species. These are usually attempts to lump species in an ecological sense and they often depend on the fishes' diet. These feeding niche groupings may then be related to the morphology and size of the fish or the prey. Food related size classes for fish have, for example, been identified by Parker and Larkin (1959), Paloheimo and Dickie (1965), and Tyler (1972). These classes are referred to as threshold lengths or feeding stanzas. Grouping of fish based on gut morphology alone has been explored extensively for flatfish by deGroot (1971), while prey size grouping was developed by Ursin (1973) and applied to northwest Atlantic fish by Hahm and Langton (1980[2]). More recently, scientists on the west coast of the United States have been looking at Pacific fish assemblages (Gabriel and Tyler 1980) and have proposed the idea of an Assemblage Production Unit (Tyler et al. in press). The Assemblage Production Unit is defined as a geographically limited natural production system of interacting organisms, in which all production is trophically linked.

The key to all these schemes of species independent linkages is a complete understanding of whatever criteria are used to group like animals. In the present paper, fish predators have been grouped by species in 5 cm size classes and the diet of each 5 cm length group described quantitatively as a percentage weight of the total stomach contents for each group. Diet overlap has then been calculated for each species-size class combination and the overlap levels related to actual diet composition. Although diet overlap calculations have their limits (discussed in Langton and Bowman 1980), as do any other methods of data reduction, this paper offers one way of evaluating real and/or potential trophic linkages between northwest Atlantic finfish.

METHODS

Stomachs were collected from both demersal and pelagic fish by personnel at the Northeast Fisheries Center Woods Hole Laboratory, as part of a multispecies food-habit study conducted from 1973 through 1976. The sampling area covered the continental shelf waters from Cape Hatteras, N.C., to the Canadian coast of Nova

---

[1] Department of Marine Resources, Marine Resources Laboratory, West Boothbay Harbor, ME 04575.

[2] Hahm, W., and R. Langton. 1980. Prey selection based on predator/prey weight ratios for some northwest Atlantic fish. Int. Counc. Explor. Sea, C.M. 1980/L:62, 9 p.

Manuscript accepted April 1982.

Scotia. Details of this food-habit survey were described in an International Council for the Exploration of the Sea document and will not be repeated here (Langton et al. 1980[3]).

Diet overlap, expressed as the percentage similarity between diets, was calculated according to the formula of Shorygin (Ivlev 1961) and has been described in several other papers as a means of evaluating the diet of northwest Atlantic finfish (Langton and Bowman 1980; Grosslein et al. 1980) although there are other methods of indexing like diets (Lipovsky and Simenstad 1978). The calculation is quite simple and is done by summing the smaller value, as a percentage weight in the present case, for all prey shared by the two predators. The computed value ranges from 0 to 100%, with 0% representing no diet overlap and 100% representing identical diets. The final overlap value is sensitive to the taxonomic level at which the prey was identified and for this paper the finest taxonomic breakdown available was used, i.e., prey identified to species whenever possible. Because of the sensitivity of this overlap measure to the taxonomic breakdown of prey, statistical methods of evaluating absolute overlap values are not practical. Instead, the values have been classified as low, 0-29%; medium, 30-60%; or high, >60% for the purpose of discussion.

The computation of diet overlap was automated and the actual computer program checked by running diet overlap for any one predator against itself. In this case the computer generates a value of 100% overlap for fish in the same size class and then a mirror image of values on each side of the 100% line. This is shown graphically in Figure 1 where Atlantic cod is plotted three dimensionally versus Atlantic cod. The plotting program only considered size classes up through class 25 (125 cm maximum fork length), but by truncating the output at this level little data was eliminated (a total of 5 cod out of 1,714 examined, for example). In fact, since the fish were taken randomly from the catch, the majority of the samples came from the most frequently occurring size classes which, even for Atlantic cod, did not approach this maximum size. Furthermore, size classes that did not include a sample size of at least 10 fish were eliminated before the data were plotted since very small samples would not necessarily be representative of the size class.

This study concentrates on two of the major fish predators in the northwest Atlantic, silver hake and Atlantic cod, and on the questions of their diet overlaps with 15 other finfish species. The food habits information presented is limited to an explanation of the prey shared by the predators which results in the observed overlap values. Detailed descriptions of the diet of the fish collected by the Northeast Fisheries Center are in preparation or have been given elsewhere. Dietary information on the northwest Atlantic Gadiformes and Pleuronectiformes can, for example, be found in Langton and Bowman (1980, 1981), Bowman and Bowman (1980), and Durbin et al. (1980)[4] while data on fish from other taxa are described in Edwards and Bowman (1979) and Grosslein et al. (1980).

RESULTS

Atlantic Cod — Little Skate

Atlantic cod, *Gadus morhua* Linnaeus, and little skate, *Raja erinacea* Mitchell, show relatively little similarity in diet (Fig. 2A). The maximum value of 48% was found for the overlap between size class 3 (11-15 cm) Atlantic cod and size class 3 little skate. The prey shared by these predators are primarily small crustaceans, in particular amphipods such as *Unciola*. Unfortunately, slightly more than 10% of the diet of each of these fish was unidentifiable with a resulting increase in the overlap values. As can be seen from Figure 2A, apart from the peak of 48%, medium levels of dietary overlap exist between Atlantic cod 11-20 cm (size classes 3 and 4) and little skate up to 45 cm total length (size class 9). Medium overlap values again occur between little skate 36-55 cm (size classes 8-11) and Atlantic cod 31-65 cm (size classes 7-13). This overlap can generally be attributed to the preponderance of a variety of crustaceans in the diet of both predators. For larger Atlantic cod the overlap values with little skate are extremely low, primarily because of a

---

[3] Langton, R., B. North, B. Hayden, and R. Bowman. 1980. Fish food habit studies-sampling procedures and data processing methods utilized by the Northeast Fisheries Center, Woods Hole Laboratory, U.S.A. Int. Counc. Explor. Sea, C.M. 1980/L:61, 16 p.

[4] Durbin, E., A. Durbin, R. Langton, R. Bowman, and M. Grosslein. 1980. Analysis of stomach contents of Atlantic cod (*Gadus morhua*) and silver hake (*Merluccius bilinearis*) for the estimation of daily rations. Int. Counc. Explor. Sea, C.M. 1980/L:60 (revised), 21 p.

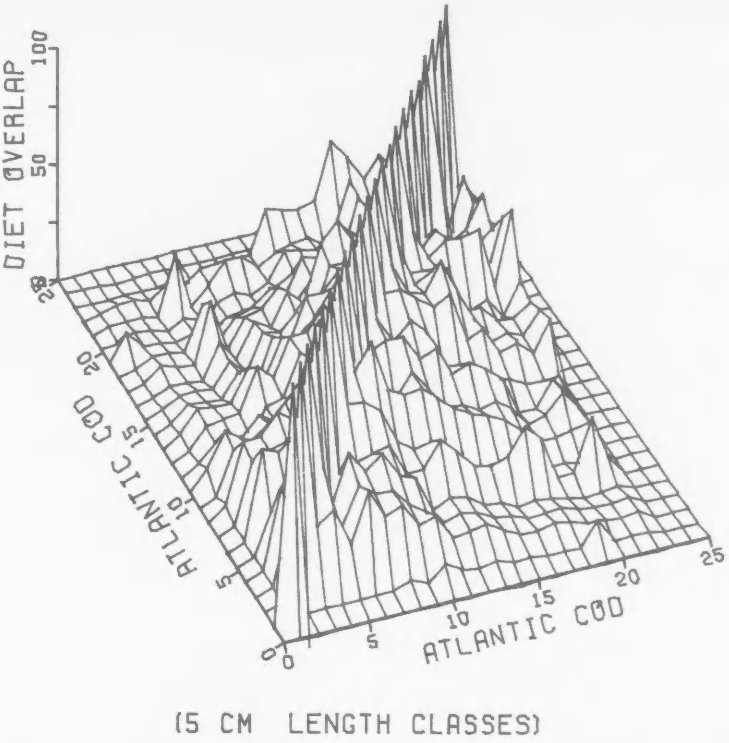


FIGURE 1.—Three dimensional plot of the diet overlap of Atlantic cod versus Atlantic cod; the same data set. Presented here is an example of the graphics output from diet similarity calculations. The peak represents 100% overlap for the same 5 cm length class of fish with a mirror image of values on either side of the peak.

shift in the diet of Atlantic cod from crustaceans to fish.

Atlantic Cod — Redfish

Atlantic cod and redfish, *Sebastes marinus* (Linnaeus), generally show low levels of diet overlap (Fig. 2B). There were, however, some medium overlap values occurring between the smaller Atlantic cod and redfish. The peak value of 49% occurred between redfish 16-20 cm (size class 4) and Atlantic cod 6-10 cm (size class 2) which was primarily the result of predation on pandalid shrimp *Dichelopandalus leptocerus*. Unfortunately, few of the redfish stomachs examined in this size class contained prey (2 out of 21 examined) so this peak may be artificially high, although in the other cases where medium overlap levels were found, pandalid shrimp were generally consumed by both predator species.

Atlantic Cod — Longhorn Sculpin

The pattern of diet overlap between Atlantic cod and longhorn sculpin, *Myoxocephalus octodecemspinosus* (Mitchill), shows low to medium overlap values over much of the size range of both species. The values do decrease, however, between the larger Atlantic cod (>61 cm, size class 13) and smaller longhorn sculpin (<16 cm, size class 3) (Fig. 2C). The peak value of 38% occurred between two different predator size classes, and in both instances the single most important prey contributing to this overlap was the

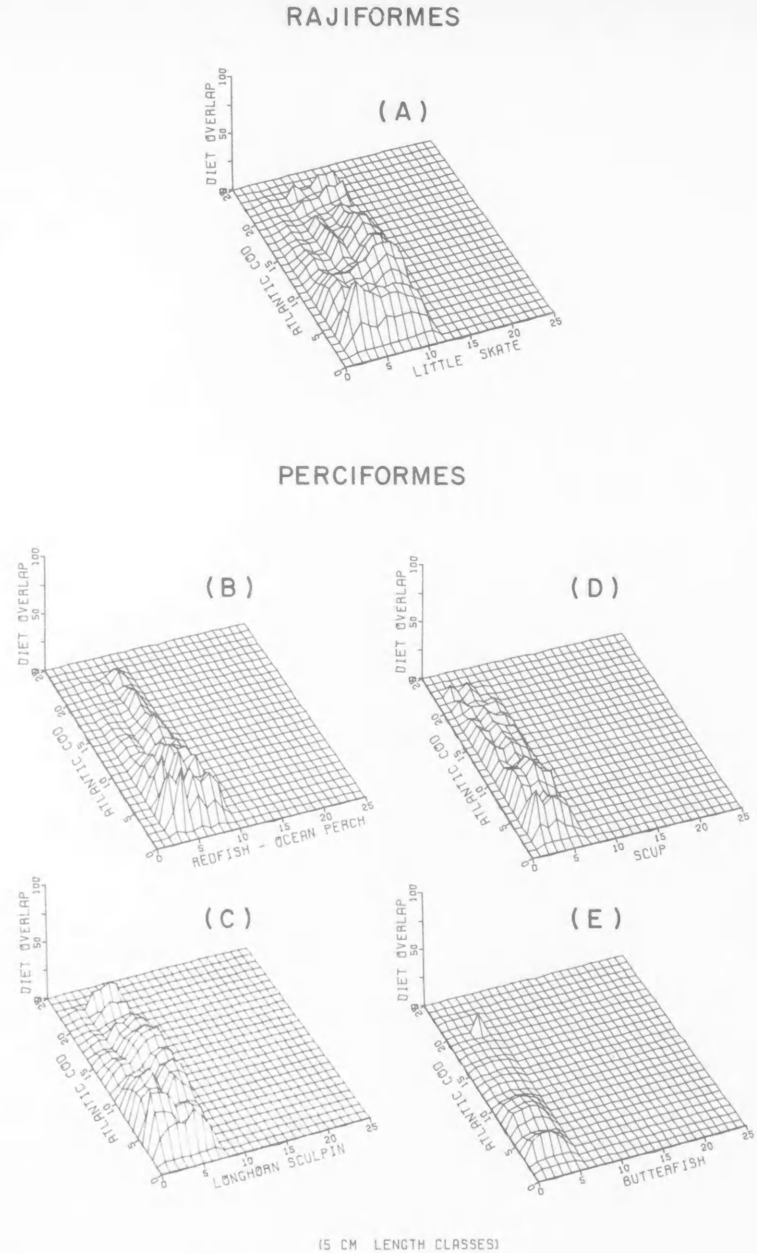


FIGURE 2.—Three dimensional plot of the diet overlap of Atlantic cod with selected rajiform and perciform fishes.

pandalid shrimp *Dichelopandalus leptocerus*, although a large variety of other crustaceans contributed to both of the predator's diets.

Atlantic Cod — Scup

Overlap between the diet of Atlantic cod and scup, *Stenotomus chrysops* (Linnaeus), is at a low level (Fig. 2D), and the low values represent a broad array of prey, principally crustaceans, that constitutes the forage base of these two predators. The only trend in these values is that they are at their lowest for large Atlantic cod (>80 cm) and all size classes of scup. This is the result of the larger Atlantic cod's piscivorous habits.

Atlantic Cod — Butterfish

The Atlantic cod and butterfish, *Peprilus triacanthus* (Peck), show very low diet overlap levels, the maximum being 19% for 11-15 cm (size class 3) fish of both species. There was, however, relatively more overlap between the smaller Atlantic cod (<45 cm) and all sizes of butterfish sampled (Fig. 2E).

Atlantic Cod — White Hake

The diet of white hake, *Urophycis tenuis* (Mitchill), shifts from crustaceans such as euphausiids, shrimp, and mysids when they are small (<≅50 cm) to primarily fish for the larger white hake. This parallels the change in the Atlantic cod's diet with size. The result is a varying degree of dietary overlap across all size classes of fish examined (Fig. 3A). Low levels occurred between the smaller white hake and the larger size classes of Atlantic cod and vice versa. Intermediate levels, values in the 30-50% range, are found in clusters which are the result of a variety of shared prey types. Some of these values in the 40 and 50% range depend upon the fish components in the diet. In particular, silver hake and herring, *Clupea harengus*, together with unidentified fish are the most commonly occurring prey that these predators share. The greatest overlaps observed were between 21-25 cm (size class 5) Atlantic cod and several larger size classes of white hake (36-85 cm, size classes 8-17) (Fig. 3A). This high overlap is somewhat artificial since it is the result of unidentified fish prey in both predators' diets. It does, however, amplify the importance of fish prey to these predators.

Atlantic Cod — Red Hake

Atlantic cod and red hake, *Urophycis chuss* (Walbaum), have low to intermediate levels of diet overlap. The lowest values occur between small red hake and large Atlantic cod (Fig. 3B). These small red hake prey quite heavily on crustaceans while the larger Atlantic cod have shifted their habits from crustacean prey to fish. The diet of red hake does, however, include more fish prey as the predators themselves grow, so that the overlap values between the larger size classes of red hake and Atlantic cod remain at an intermediate level.

Atlantic Cod — Spotted Hake

Atlantic cod and spotted hake, *Urophycis regia* (Walbaum), have diets which overlap at low to intermediate levels (Fig. 3C). The prey that they have in common is primarily crustaceans but may also include some fish. The cluster of intermediate values occurring between 11-25 cm (size classes 3-5) Atlantic cod and 11-30 cm (size classes 3-6) spotted hake is, for example, the result of predation on crustaceans such as *Meganyctiphanes*, *Dichelopandalus*, *Crangon*, *Unciola*, and other less significant taxa, while the intermediate overlap peaks between 31-35 cm spotted hake and Atlantic cod are due to fish predation.

Atlantic Cod — Pollock

Atlantic cod and pollock, *Pollachius virens* (Linnaeus), show low to intermediate levels of diet overlap over all size classes of both predators examined. Both of these species are crustacean/fish predators, relying more heavily on fish as they increase in size. For the smaller pollock, the euphausiid *Meganyctiphanes norvegica* and the shrimp *Pasiphaea multidentata* were the major components of the diet while the Atlantic cod relied on a much broader variety of prey. For the larger fish of both species a variety of pisces were included in the diet, some of which was not readily identifiable at any lower level than simply fish flesh. The problem in identifying fish remains generated two artificial peaks in overlap

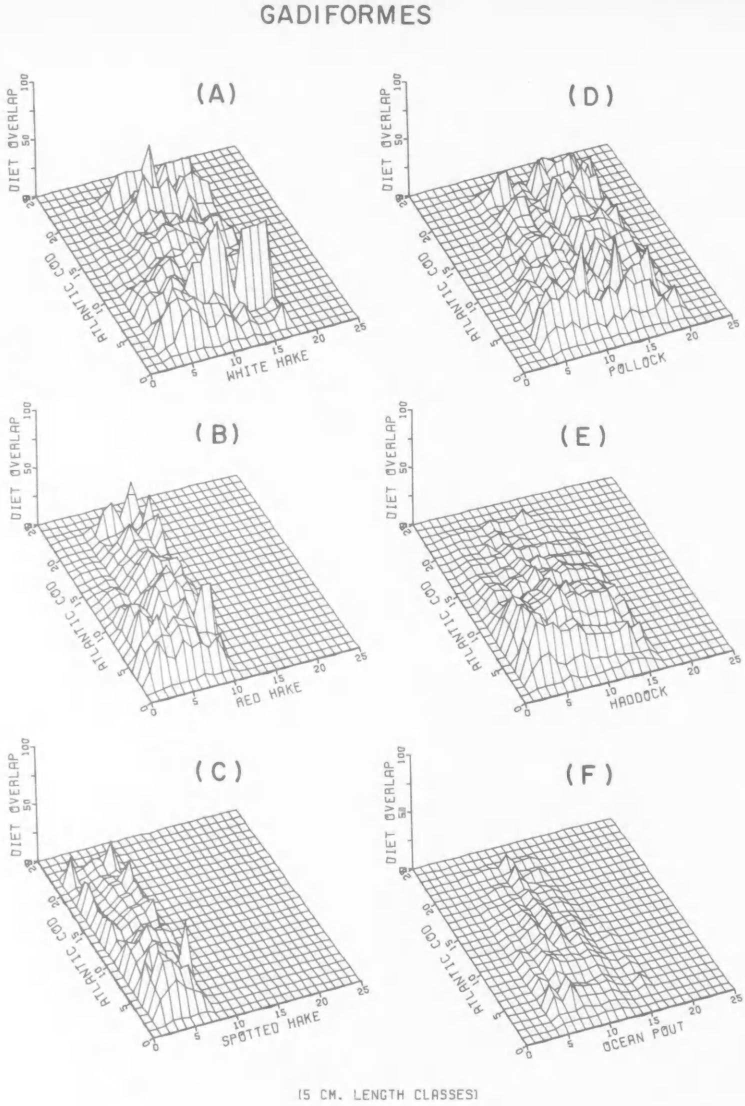


FIGURE 3.—Three dimensional plot of the diet overlap of Atlantic cod with selected gadiform fishes.

between Atlantic cod of size class 5 and pollock of size classes 10 and 14 as seen in Figure 3D.

Atlantic Cod — Haddock

Haddock, *Melanogrammus aeglefinus* (Linnaeus), is primarily benthic in its feeding habits with the result that its diet is similar to Atlantic cod's only when the Atlantic cod are also feeding on the benthos. Consequently, the degree of diet overlap between these two predators is highest for the smaller animals, as can be seen in Figure 3E. The diversity of prey that both these predators consume reduces the computed overlap values. The relatively low maximum values, 47% being the highest for 16-20 cm (size class 4) Atlantic cod and 11-15 cm (size class 3) haddock, make it difficult to identify any particular species of prey that gives rise to the observed intermediate levels of overlap.

Atlantic Cod — Ocean Pout

Ocean pout, *Macrozoarces americanus* (Schneider), are fairly specific in their predatory habits, and these habits do not overlap with those of Atlantic cod to any extent (Fig. 3F). A single prey species, the sand dollar, *Echinarachnius parma*, accounts for most of the diet of ocean pout although amphipods were also present in many of the fish stomachs examined.

Atlantic Cod — American Plaice

The diets of Atlantic cod and American plaice, *Hippoglossoides platessoides* (Fabricius), overlap at quite low levels, the highest value being 33% for 26-30 cm (size class 6) Atlantic cod and 21-25 cm (size class 5) American plaice. American plaice prey on a variety of benthic animals but, as they grow larger, they rely more on echinoderms than crustaceans and polychaetes. This is reflected in the diet overlap plot (Fig. 4A); the larger size classes of American plaice (>45 cm) have extremely small overlap with Atlantic cod because of predation on the sand dollar.

Atlantic Cod — Witch Flounder

Little diet overlap occurs between Atlantic cod and witch flounder, *Glyptocephalus cynoglossus* (Linnaeus), with all of the calculated values being 30% or less (Fig. 4B). Witch flounder are benthic predators with polychaete worms being of major importance as prey although they do consume crustaceans and other invertebrates. It is the crustacean component of the diet which accounts for these low levels of overlap with the Atlantic cod.

Atlantic Cod — Yellowtail Flounder

The diets of Atlantic cod and yellowtail flounder, *Limanda ferruginea* (Storer), overlap at generally low levels (Fig. 4C). There is only one cluster of intermediate levels involving yellowtail flounder from a single size class (class 3, 11-15 cm) which reflects the occurrence of pandalid shrimp *Dichelopandalus leptocerus* in both predators' diets. As with many other species, a reduction in the level of overlap occurs as the disparity in fish size increases. For yellowtail flounder this is quite apparent when compared with the larger Atlantic cod because the large Atlantic cod are primarily piscivorous. However, this reduction is not as noticeable for large yellowtail flounder and small Atlantic cod since the benthic habits of yellowtail flounder change little as the fish increase in size.

Atlantic Cod — Fourspot Flounder

Atlantic cod and fourspot flounder, *Paralichthys oblongus* (Mitchill), show low and intermediate levels of diet overlap (Fig. 4D) which is primarily a result of predation on crustaceans. The single most important crustacean prey was the pandalid shrimp *Dichelopandalus leptocerus* which makes up from 17% to 30% of the diet of 21-30 cm fourspot flounder and 3% to 40% of the diet of 6-45 cm Atlantic cod.

Silver Hake — Little Skate

The pattern of diet overlap between silver hake, *Merluccius bilinearis* (Mitchill), and little skate is shown in Figure 5A. Generally, overlap levels are low but medium levels range up to a high of 44% between small silver hake 1-15 cm (size classes 1-3) and little skate 11-45 cm total length (size classes 3-9). This degree of overlap can be attributed to the crustaceans in each of these predators' diets with the sand shrimp, *Crangon septemspinosa*, being of particular importance. For larger silver hake the diet overlap with little skate is insignificant since these larger hake prey on fish while little skate of all sizes prey primarily on benthic crustaceans.

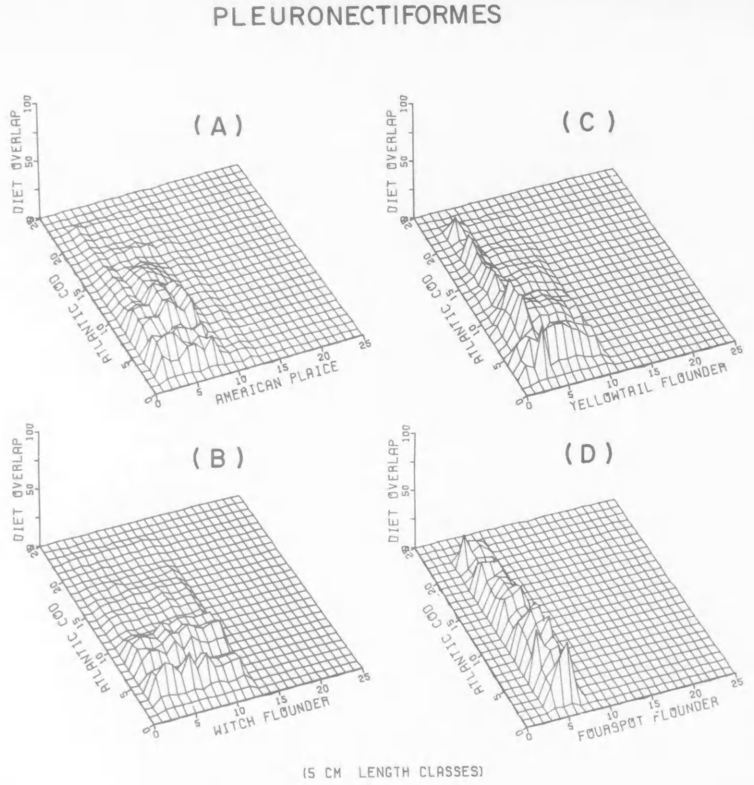


FIGURE 4.—Three dimensional plot of the diet overlap of Atlantic cod with selected pleuronectiform fishes.

Silver Hake — Redfish

High levels of overlap occur between 16-20 cm (size class 4) silver hake and 11-45 cm (size classes 3-9) redfish (Fig. 5B). The peak value is 75% for 31-35 cm (size class 7) redfish and these smaller silver hake. Most of this overlap is due to predation on the euphausiid *Meganyctiphanes norvegica*, which accounted for 60% and 63% of the diet of these 16-20 cm silver hake and 31-35 cm redfish, respectively. The other high overlap values between these two predators can also be attributed to euphausiids making up more than 50% of the diets. Medium levels of overlap, 30-42%, were found for other size silver hake and redfish. Once again *Meganyctiphanes norvegica* was a major dietary item but in some cases *Dichelopandalus leptocerus* also contributed significantly. For the larger silver hake (>35 cm, greater than size class 7) there was little, if any, diet overlap. These large silver hake prey heavily on fish while redfish are predominantly crustacean predators.

Silver Hake — Longhorn Sculpin

Intermediate diet overlap values occur between silver hake ranging from 6 to 15 cm in length (size classes 2-3) and most of the size classes of longhorn sculpins examined (Fig. 5C). This overlap is due to both predators' reliance on crustaceans such as *Crangon septemspinosa*, *Dichelopandalus leptocerus*, and *Neomysis americana*. For the larger silver hake, those that are primarily piscivorous, there is virtually no over-

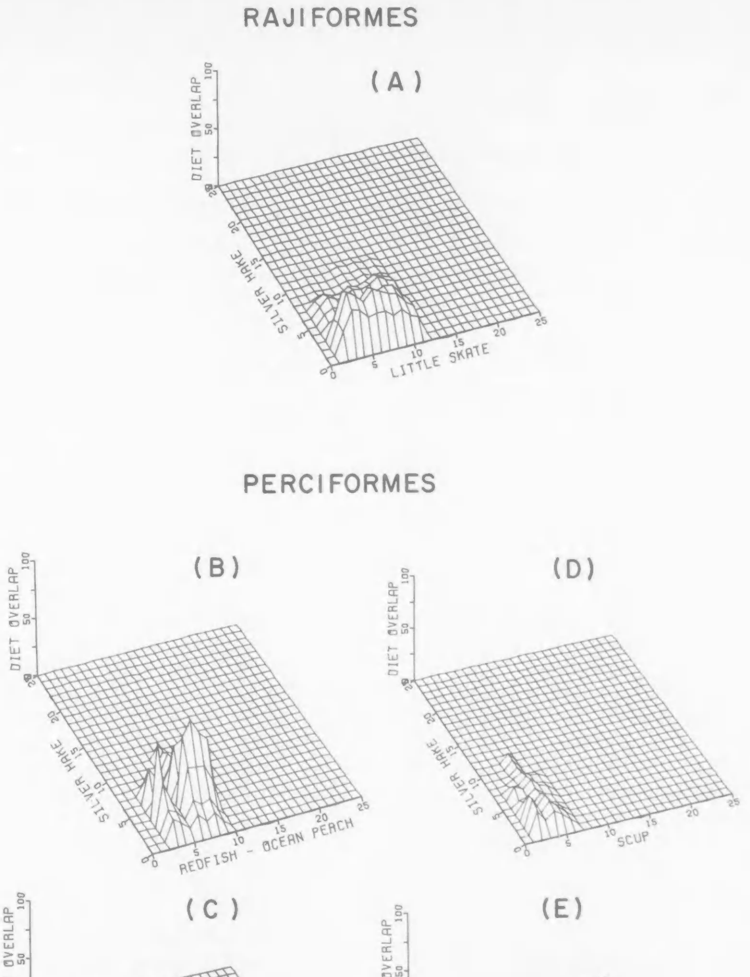


FIGURE 5.—Three dimensional plot of the diet overlap of silver hake with selected rajiform and perciform fishes.

lap or, at least, extremely low levels of overlap with longhorn sculpin.

Silver Hake — Scup

Silver hake and scup both prey on crustaceans, but they share few prey species in common so that diet overlap values are quite low (Fig. 5D). There is a trend for the overlap values to decrease when comparing larger silver hake and scup which mirrors the shift towards fish predation by these larger silver hake.

Silver Hake — Butterfish

The diets of silver hake and butterfish overlap at very low levels, the highest value being 17% which was the result of predation on the squid *Loligo* (Fig. 5E). Generally, the butterfish is more planktonic in its predatory habits than the silver hake which is reflected in the low overlap values.

Silver Hake — Atlantic Cod

Silver hake and Atlantic cod are generally found to have low to intermediate levels of diet overlap and very few values that are >60% (Fig. 6A). All of the high values are the result of unidentified fish remains forcing up the computed overlap values. Both of these predators become more piscivorous as they grow larger, but this size-specific dietary shift is not reflected in an obvious change in the level of diet overlap. In other words, the smaller fish share crustacean prey species such as euphausiids while the larger predators both prey on a number of different species of fish.

Silver Hake — White Hake

There is a clear pattern of overlap when comparing the diets of silver and white hake (Fig. 6B). The diets of the larger fish of both species do not overlap with the smaller fish of the opposite species. In other words, the diet of small silver hake has little in common with the larger white hake and vice versa. The explanation for this is a size dependent change in diet for both predators. When small, they both rely on crustaceans, such as euphausiids, and then gradually shift to fish as the predator grows. For example, the high value, 74% between 16-20 cm (size class 4) silver hake and 31-35 cm (size class 7) white hake results from over 50% of either of these predators feeding on *Meganyctiphanes norvegica*. For comparison, the other high value, 75%, for 41-45 cm (size class 9) silver hake and 66-70 cm (size class 14) white hake, is the result of fish predation on such fish as silver hake, clupeids, and other unidentifiable fish remains.

Silver Hake — Red Hake

The diet overlap between silver and red hake ranges from 0% to intermediate levels as high as 56%. The general pattern is increasing overlap with increasing predator size up to 26-30 cm (size class 6) and then leveling off or decreasing slightly between the larger fish (Fig. 6C). The peak value, occurring between 26-30 cm silver hake and 41-45 cm (size class 9) red hake, can be explained by predation on fish, *Dichelopandalus leptocerus*, and other invertebrates.

Silver Hake — Spotted Hake

Silver and spotted hake show, for the most part, intermediate to high levels of diet overlap between similar size fish (Fig. 6D). Peak values of 60% and 70% occur, for example, between 11-20 cm (size classes 3-4) and 16-25 cm (size classes 4-5) silver and spotted hake, respectively. These peaks are the result of a reliance by both predators on *Meganyctiphanes norvegica*, *Dichelopandalus leptocerus*, and *Crangon septemspinosa*. The intermediate overlap values are also, however, a reflection of predation on fish, especially for the larger silver and spotted hake.

Silver Hake — Pollock

High diet overlap values exist between silver hake 16-20 cm (size class 4) and pollock 16-65 cm (size classes 4-13). Two prey categories are responsible for these high levels, *Meganyctiphanes norvegica* and unidentified fish remains. Medium levels of overlap between these two predators are common for most size classes except for silver hake below 10 cm. Overlap between these smaller silver hake and all sizes of pollock falls into the lower overlap category. There are also extremely low values between small pollock and large silver hake (Fig. 6E).

Silver Hake — Haddock

Silver hake and haddock show little similarity in their diets and the resulting diet overlap val-

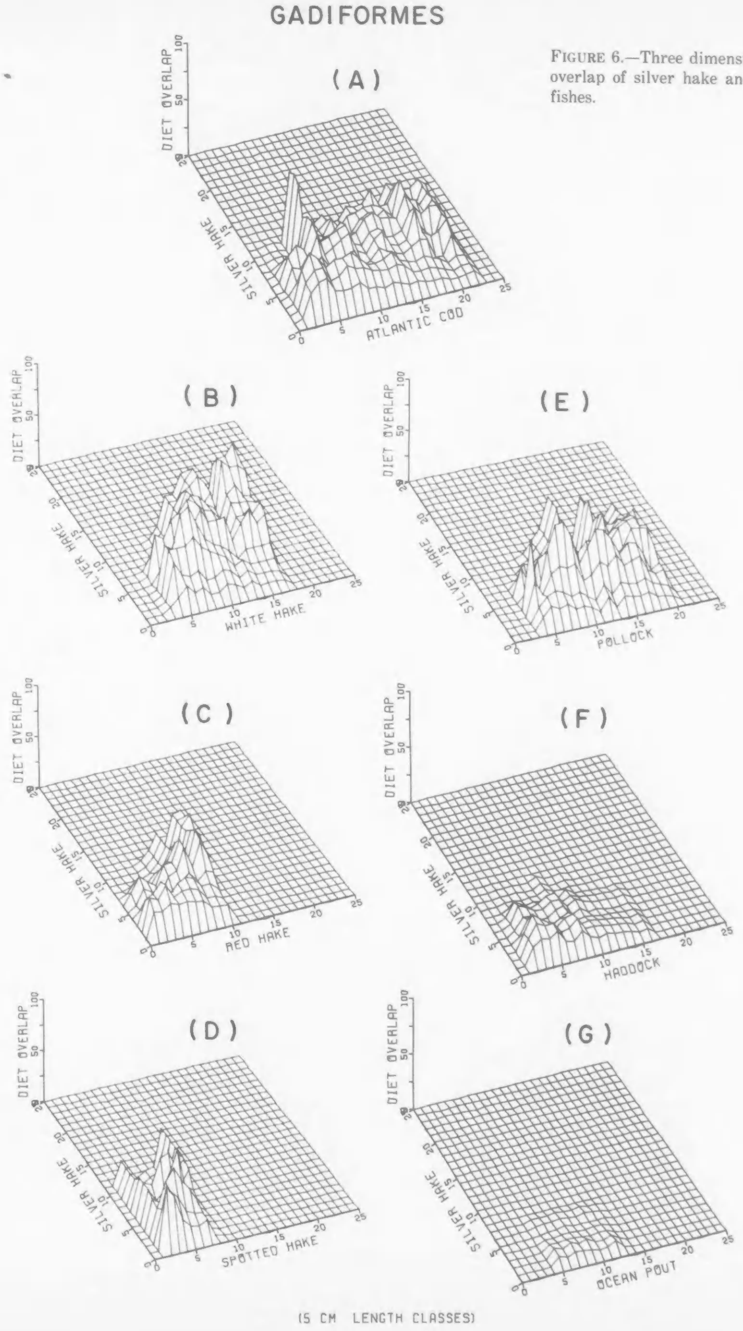


FIGURE 6.—Three dimensional plot of the diet overlap of silver hake and selected gadiform fishes.

ues are all quite low (Fig. 6F). Even with these low values, there is an obvious trend; the higher values occur between the smaller individuals of these two predators which reflects the dependance of small silver hake and haddock on crustacean prey.

Silver Hake — Ocean Pout

The diets of silver hake and ocean pout are mutually exclusive so that there is an extremely small degree of diet overlap (Fig. 6G). The only prey that they share in common are amphipods, but again, this is at a very low level.

Silver Hake — American Plaice

Silver hake and American plaice show very low levels of dietary overlap (Fig. 7A). Despite the lack of diet similarity, a pattern does emerge when comparing these two predators. The larger size classes of both species show virtually no overlap, while what similarity does exist occurs between silver hake and American plaice <40 cm. The diet of these larger individuals is quite specific, fish for silver hake and echinoderms for American plaice, so little overlap is to be expected, while the smaller individuals of both species prey on invertebrates.

Silver Hake — Witch Flounder

Silver hake and witch flounder share little prey in common with resulting low levels of diet overlap. The only exception to these low levels is a high peak (66% and 67%) between 16-20 cm (size class 4) silver hake and 11-20 cm (size classes 3-4) witch flounder (Fig. 7B). A single prey species,

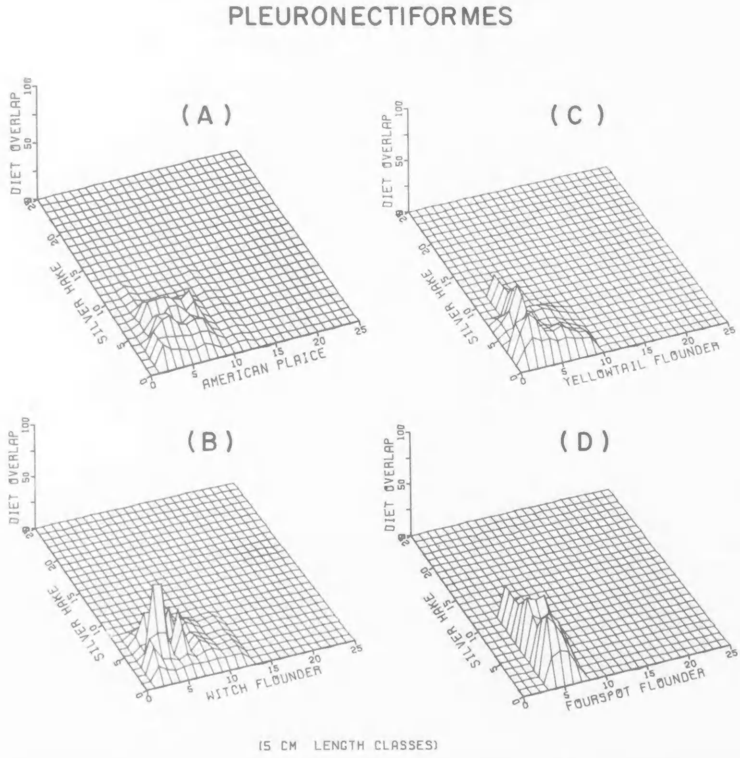


FIGURE 7.—Three dimensional plot of silver hake and selected pleuronectiform fishes.

Meganyctiphanes norvegica, is responsible for this since it alone accounts for >63% of each predator's diet. Similarly, the smaller peaks in the figure are also the result of having euphausiids as a common prey item.

Silver Hake — Yellowtail Flounder

Silver hake and yellowtail flounder have, for the most part, low levels of diet overlap (Fig. 7C). The few intermediate levels that do occur are, in all but one instance, related to yellowtail flounder that are 11-15 cm in length (size class 3) which have preyed on *Crangon septemspinosa*, *Dichelopandalus leptocerus*, or small unidentified fish. The one exception is for 6-10 cm (size class 2) yellowtail flounder and silver hake. These fish preyed primarily on *Crangon septemspinosa*, *Neomysis americana*, and amphipods with a resulting diet overlap of 39%. Even with these low overlap levels an overall pattern is apparent; the greatest overlap occurs between the smaller size classes of both species.

Silver Hake — Fourspot Flounder

The diets of silver hake and fourspot flounder overlap at low to intermediate levels (Fig. 7D). The highest value, 54%, occurs between 6-10 cm (size class 2) silver hake and 16-20 cm (size class 4) fourspot flounder. The peak, as with most of the other intermediate values, is the result of predation on crustaceans such as *Crangon septemspinosa*, *Neomysis americana*, and *Dichelopandalus leptocerus*.

DISCUSSION

The diet overlap comparisons presented here are one way to simplify fish food habits data and to identify real or, at least, potential pathways of energy exchange. As with any method of data reduction, however, certain compromises have to be accepted which must be kept in mind when discussing the results. The limitations of percentage similarity calculations have been described by several authors (Day and Pearcy 1968; Moyle 1977; Keast 1977; Langton and Bowman 1980; MacPherson 1981) and these limits include both biotic and abiotic factors. Such factors as the taxonomic level of prey identification, the actual quantity of prey consumed (especially since percentage similarity is a relative measure of dietary constituents), predator/prey distribution and abundance, and temporal factors that influence both predator and prey behavior all have to be considered in evaluating the meaning of diet overlap data.

The present data consider the entire northwest Atlantic as a single homogeneous ecological system since all the available data were grouped by species for the diet overlap calculations. This is a first attempt to examine size-specific finfish predation in the northwest Atlantic and, without more extensive basic biological information on finfish and invertebrate community structure, there was no reason to subdivide the data set. The research survey cruises on which the fish stomachs were collected were, however, planned for discrete geographic regions (e.g., Gulf of Maine, Georges Bank) and employed stratified random sampling based primarily on depth dependent strata (Grosslein 1969; Clark and Brown 1977). If the research survey catch data were analyzed statistically, using techniques such as cluster analysis, to identify fish species associations or assemblages, then there may be justification for subdividing the data set. Such methods have been utilized recently to identify northwest Pacific finfish assemblages (Gabriel and Tyler 1980; Tyler et al. in press) and have been used, to a limited degree, for northwest Atlantic fishes (Tyler 1972, 1974; Knight and Tyler 1973). Whatever techniques are employed the basic problem is the same: defining what constitutes an ecologically homogeneous system.

From the figures presented, it is clear that completely dissimilar diets occur very rarely. This raises the question of the significance of diet overlap and whether such measures are indicative of resource competition. The limits of diet overlap calculations have been dealt with briefly above and the significance of any given numerical value for diet overlap has also been mentioned. Diet overlap has some value as an indicator of potential energy flow pathways but it is not an absolute measure of trophic linkages. The overlap values are obviously indicators of coexistence rather than competition, especially since overlap values have been observed to decrease rather than increase when resources are limited (Zaret and Rand 1971; Keast 1978; MacPherson 1981). The ideas of competition versus coexistence have been considered for gadoid fishes by Jones (1978). Jones pointed out some of the more subtle distinctions between the diets of three gadoid species which, on cursory examination, appear to overlap. For example, although both haddock and Atlantic cod from the same trawl haul preyed on juvenile *Sebastes*, they were preying on different-sized juveniles and, in general, Jones observed that Atlantic cod tended to consume larger prey than haddock of the same size. This type of detailed stomach contents analysis, together with observations on fish feeding behavior in the laboratory and in situ, is the type of biological information necessary for accurately defining what constitutes an ecologically homogeneous system, or, more importantly, an energetically coupled unit within the system.

There are some general patterns to the overlap values which may indicate real, or at least potential, trophic linkages. In comparing Atlantic cod with six other gadids, for example, the overlap levels generally are at their lowest between the larger cod (greater than size class 10, >50 cm) and the smaller size classes of the other predators (Fig. 3). This reflects the shift in the Atlantic cod's feeding habits from being primarily a crustacean predator to a piscivore with an increase in body size. In effect, Atlantic cod occupy different, size-specific, feeding niches which correspond to these other predators only when both species are small and more dependent on crustacean prey. For silver hake (Fig. 6) the pattern is similar but silver hake are a smaller fish than Atlantic cod and switch to a piscivorous habit at a smaller size. In addition to this pattern, there is also a noticeable shift in overlap between silver hake, the three other hake species, and pollock. The overlap with the smaller size classes of silver hake is low or even decreases slightly as the four other gadid species increase in size. Conversely, overlap is highest for the larger silver hake and these four gadids. This is a result of predation on many different species of crustaceans by all these predators and a shift towards fish predation as they grow.

In comparing both Atlantic cod and silver hake with the one rajiform and the four perciform fish species, the overall pattern of diet overlap is the same. The larger Atlantic cod and silver hake show a decreasing level of overlap with the smaller size classes of these other finfish predators (Figs. 2, 5). Atlantic cod and silver hake do not show a similar pattern of diet overlap when compared with the four pleuronectiform species of finfish (Figs. 4, 7). With the three pleuronectid species (Fig. 4A-C) the highest levels of overlap with Atlantic cod occur between the smaller size classes of all three species while the lowest levels occur between the larger size classes. This is similar to changes in overlap observed for the perciform species. For the one bothid (Fig. 4D) a size-dependent shift in overlap is not readily apparent. The overlap values for silver hake and flatfishes are at a maximum, albeit low overall, for the smaller individuals of the three pleuronectids (Fig. 7A-C) but, like the Atlantic cod, are fairly constant over all size classes of the one bothid species examined (Fig. 7D). This pattern of diet overlap with the pleuronectids may be attributed to the crustacean/fish shift in diet for the Atlantic cod and silver hake, and either little change in the flatfish diet or, as with American plaice, a change in diet to one that does not include much, if any, fish prey.

Atlantic cod and silver hake are crustacean/fish predators with a size-dependent shift in predation from crustaceans to fish as these predators grow. In the present data the shift to fish predation for Atlantic cod occurs at about 60-70 cm and for silver hake at about 20-25 cm. These sizes are not absolute and depend very much on the availability of prey. Daan (1973), for example, observed a difference in North Sea cod feeding habits when comparing samples from the northern and southern North Sea. Crustaceans predominated in the stomachs of the larger specimens from the southern region while their northern counterparts had already shifted over to a piscivorous habit. In the northwest Atlantic a similar, but less obvious, shift was observed in the diet of cod when compared over a 10-yr period (Grosslein et al. 1980). When the finfish biomass was low (1973-76 vs. 1963-66), crustaceans were slightly more important as prey although the general impression resulting from studying the two data sets was a fairly constant pattern of predation over time. The diets of Atlantic cod, and presumably most of these other predators, are fairly stable although there is an apparent degree of fine tuning that depends upon the availability of prey and other controlling factors in the environment.

In summary, assuming that the diets of Atlantic cod and silver hake are reasonably stable over time, and that the same is true for the 15 other predators examined, then the pattern of overlap described above suggests that the greatest overall potential for interaction exists between the smaller stages of the two gadids and the other predators. Furthermore, the greatest overlap, with few exceptions, occurs among the gadiform fishes themselves rather than between the gadids and the other ordinal taxonomic levels.

This observation may not only be reassuring to the taxonomist but is also of significance to fishery biologists in their attempts to identify ecological units. It suggests that future food habit studies should be directed towards the juvenile, or at least smaller, stages of closely related species if the goal is to understand how finfish coexist by partitioning food resources in the marine environment.

ACKNOWLEDGMENTS

My sincerest thanks go to the people who helped generate the diet overlap data described in this paper: Bill Freund, Woods Hole Oceanographic Institution, wrote the computer program that automated the diet overlap calculations; Jacki Murray and John Hauser, Northeast Fisheries Center, modified the program and generated most of the data; Jean Garside and Margaret Hunter, Department of Marine Resources, developed the three dimensional plotting program and generated the figures for the paper.

LITERATURE CITED

BOWMAN, R. E., AND E. W. BOWMAN.
1980. Diurnal variation in the feeding intensity and catchability of silver hake (*Merluccius bilinearis*). Can. J. Fish. Aquat. Sci. 37:1565-1572.

CLARK, S. H., AND B. E. BROWN.
1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1973-74, as determined from research vessel survey data. Fish. Bull., U.S. 75:1-21.

DAAN, N.
1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Neth. J. Sea Res. 6:479-517.

DAY, D. S., AND W. G. PEARCY.
1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. J. Fish. Res. Board Can. 25:2665-2675.

DEGROOT, S. J.
1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. 5: 121-196.

EDWARDS, R. L., AND R. E. BOWMAN.
1979. Food consumed by continental shelf fishes. *In* H. Clepper (editor), Predator-prey systems in fisheries management, p. 387-406. Sport Fishing Inst., Wash., D.C.

GABRIEL, W. L., AND A. V. TYLER.
1980. Preliminary analysis of Pacific coast demersal fish assemblages. Mar. Fish. Rev. 42(3-4):83-88.

GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

GROSSLEIN, M. D., R. W. LANGTON, AND M. P. SISSENWINE.
1980. Recent fluctuations in pelagic fish stocks of the Northwest Atlantic, Georges Bank region, in relation to species interactions. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 177:374-404.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, 302 p.

JONES, R.
1978. Competition and co-existence with particular reference to gadoid fish species. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 172:292-300.

KEAST, A.
1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environ. Biol. Fishes 2:53-70.
1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environ. Biol. Fishes 3(1):7-31.

KNIGHT, W., AND A. V. TYLER.
1973. A method for compression of species association data by using habitat preferences, including an analysis of fish assemblages on the southwest Scotian Shelf. Fish. Res. Board Can. Tech. Rep. 402, 15 p.

LANGTON, R. W., AND R. E. BOWMAN.
1980. Food of fifteen northwest Atlantic gadiform fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-740, 23 p.
1981. Food of eight northwest Atlantic pleuronectiform fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-749, 16 p.

LIPOVSKY, S. J., AND C. A. SIMENSTAD (editors).
1978. "Gutshop 78" fish food habits studies. Proceedings of the Second Pacific Northwest Technical Workshop, 222 p. Washington Sea Grant Publication, Division of Marine Resources, University of Washington, Seattle, WA 98195.

MACPHERSON, E.
1981. Resource partitioning in a Mediterranean demersal fish community. Mar. Ecol. Prog. Ser. 4:183-193.

MOYLE, P. B.
1977. In defense of sculpins. Fisheries (Bethesda) 2: 20-23.

PALOHEIMO, J. E., AND L. M. DICKIE.
1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Board Can. 22:521-542.

PARKER, R. R., AND P. A. LARKIN.
1959. A concept of growth in fishes. J. Fish. Res. Board Can. 16:721-745.

TYLER, A. V.
1972. Food resource division among northern marine, demersal fishes. J. Fish. Res. Board Can. 29:997-1003.
1974. Community analysis. *In* R. O. Brinkhurst, Chapter 5, The benthos of lakes, p. 65-84. St. Martin's Press, Inc., N.Y.

TYLER, A. V., W. L. GABRIEL, AND W. J. OVERHOLTZ.
In press. Adaptive management based on structure of fish assemblages of northern continental shelves. Can. J. Fish. Aquat. Sci.

URSIN, E.
1973. On the prey size preference of cod and dab. Danish Inst. Fish. Mar. Res. 7:85-98.

ZARET, T. M., AND A. S. RAND.
1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336-342.

THE RELATIONSHIP OF WINTER TEMPERATURE AND SPRING LANDINGS OF PINK SHRIMP, *PENAEUS DUORARUM*, IN NORTH CAROLINA[1]

WILLIAM F. HETTLER AND ALEXANDER J. CHESTER[2]

ABSTRACT

Spring landings of pink shrimp in North Carolina were highly correlated with water temperature during the previous winter. The strongest relation was found between landings and the average water temperature of the two coldest consecutive weeks of each year ($r^2 = 0.82$). Following the cold winters of 1977, 1978, 1980, and 1981, when temperatures averaged below 5°C, landings were <160,000 kg. Following the warm winters of 1965, 1974, and 1975, when temperatures averaged above 8°C, landings were >450,000 kg. Changes in water temperature through the year were described by a sine-cosine curve in which minimum temperatures generally occurred during the 5th week and maximum temperatures occurred during the 31st week of the year. Weekly mean air temperatures were linearly related to water temperatures ($r^2 = 0.97$) over the entire range of data, but they were not useful as proxy data for predicting pink shrimp landings ($r^2 = 0.50$) because the air-water relation was more variable at low temperature. Local rainfall did not have a significant effect on shrimp landings.

Temperature is a critical environmental factor influencing metabolism, growth, reproduction, distribution, and survival of animals (Kinne 1963). Local abundance may be affected by migration or death in response to extreme deviations from temperatures to which the animal is adapted. The effect of such temperature extremes is expected to be more severe for a population at the limit of its geographic range, particularly when temperature is known to be a factor limiting north-south distribution (Williams 1969a).

For species whose life cycle is completed in 1 yr, or in fisheries where reliance on annual recruitment is heavy (Loucks and Sutcliffe 1978), temperature records may be useful as a predictor of landings. A cause-and-effect relationship between harvest and temperature may be more obvious for species with one year class than for long-lived species whose landings are complicated by multiple year-class contributions (Norcross and Austin 1981). Penaeid shrimp, which have an annual life cycle, have no significant contribution from other year classes to compensate for a reduction in biomass caused by unfavorable temperatures.

Shrimp mortality in the southeast United States due to cold has been reported by Gunter and Hildebrand (1951), Lindner and Anderson (1956), and Lunz (1958). Of the three species of *Penaeus* that occur in North Carolina waters, only pink shrimp, *Penaeus duorarum* Burkenroad, overwinter in shallow estuaries (Williams 1955a) and, therefore, would be more likely to suffer from abnormally cold winter temperatures than either brown shrimp, *P. aztecus*, or white shrimp, *P. setiferus*. Pink shrimp have an annual life cycle in which the adults spawn offshore during early summer and postlarvae and juveniles utilize the estuaries, where several environmental factors can affect distribution and survival. These factors include temperature, salinity, substrate, debris cover, and seagrass species and density (Costello and Allen 1970; Grady 1971; Gunter 1950, 1961; Williams 1955a, 1958, 1969b). Peak recruitment of postlarvae into North Carolina estuaries occurs from July to September (Williams 1969b). Juveniles that overwinter in the estuary migrate towards the sea as adults, primarily in May and June, and become the object of a trawl and channel net fishery located in the mouth of the Neuse River, southwestern Pamlico Sound, Core Sound, Bogue Sound, and in the ocean between Beaufort Inlet and Bogue Inlet (Williams 1955b).

The primary purpose of this study was to investigate the relationship between winter tem-

---

[1] Contribution No. 82-12B of the Southeast Fisheries Center, National Marine Fisheries Service, NOAA.

[2] Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

Manuscript accepted March 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

peratures and spring landings of pink shrimp in North Carolina to determine if temperature could be used as a predictor of landings. Several recent harsh winters (Diaz and Quayle 1980; Ingham 1979) provided an opportunity to compare landings over a range of temperatures. This relationship may serve to focus attention on the importance of temperature extremes in understanding ecosystem productivity. We also analyzed available water and air temperatures to model the annual temperature in the lower Newport River estuary, to compare the weekly mean temperatures of each year with the annual model, and to test the use of air temperature as proxy data for periods when no water temperatures were available. Finally, we examined the effect of local winter rainfall on pink shrimp landings.

METHODS

Temperature records were analyzed from the Newport River estuary, which is centrally located within the North Carolina pink shrimp nursery and fishing grounds, the "Carteret-Onslow Area" of Williams (1955b) (Fig. 1). This estuary had been the site of several studies conducted by our laboratory during which temperatures were routinely monitored at one or more locations, but the entire time-series of temperature records had not been analyzed.

Seawater temperatures were obtained from recordings made at Pivers Island near Beaufort, N.C., at the mouth of the Newport River estuary beginning in 1962. From 1962 until 1968, records were kept on the island's north channel, and from 1968 to the present, records were kept on the east channel. These locations are <400 m apart. From 1968 to mid-1974, continuous records either were not kept or were inadvertently lost. Thus, complete continuity from 1962 to 1981 was not possible.

Seawater temperature was recorded continuously on 7-d circular charts. Recordings since 1974 were calibrated (±0.1°C) with a precision mercury thermometer. The accuracy and precision of pre-1974 records could not be determined. Weekly means from 1962 to mid-1974 were calculated by averaging hourly readings during each 7-d cycle. Weekly means from mid-1974 to 1981 were calculated by using a compensating polar planimeter. The planimeter method permitted rapid integration of the entire weekly temperature record into a single temperature by converting the mean radius of the area encompassed by the temperature cycle to the equivalent weekly mean temperature.

Daily air temperatures and monthly precipitation totals were recorded at the National Weather Service observation station in Morehead City, N.C., 6.2 km west of Pivers Island, and were pub-

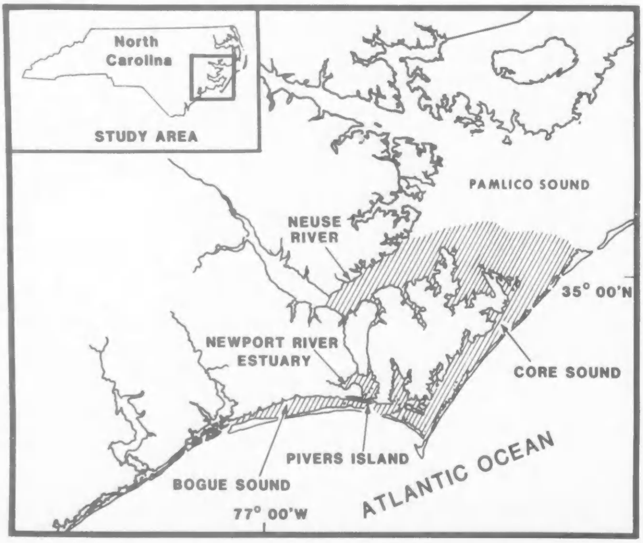


FIGURE 1.—Pink shrimp nursery area (indicated by hatched lines). Pivers Island was point-source of water temperature data.

lished by NOAA Environmental Data and Information Service, National Climatic Center, Asheville, N.C. Weekly mean air temperatures were calculated by averaging daily maximum and minimum records. Rainfall records for December, January, and February were totalled for each winter.

The commercial landings of pink shrimp (kilograms of abdomens) were obtained from records published by the U.S. Department of Commerce (North Carolina Shrimp Landings, Current Fisheries Statistics series) (Table 1). Landings from late winter through July of each year comprised the portion of the fishery considered by our hypothesis to be influenced by severe overwintering conditions, primarily extensive periods of low temperatures and, possibly, reduced salinities. Landings after July were excluded because, in late summer, size and weight decreased, reflecting recruitment of postwinter juveniles into the estuary.

RESULTS AND DISCUSSION

Annual Temperature Cycle in the Newport River Estuary

Weekly mean water temperatures in the Newport River estuary displayed a basically sinusoidal annual pattern (Fig. 2). Actually there appeared to be a slight distortion in the seasonal sine relationship whereby vernal warming proceeded at a slower rate than autumnal cooling. Available data from 1962 to 1981 were used to mathematically define the annual temperature cycle according to the following least-squares, multiple regression equation:

$$T_W = a + b_1 \text{ SIN } \left(\frac{2\pi W}{52}\right) + b_2 \text{ COS } \left(\frac{2\pi W}{52}\right),$$

where T_W was the mean weekly temperature for week W, a was an intercept reflecting the overall average yearly temperature, and b_1 and b_2 were regression coefficients controlling the timing and amplitude of annual minimum and maximum temperatures.

The derived equation (Fig. 2) was an adequate representation of the annual cycle of temperature in the Newport River estuary ($R^2 = 0.93$) and helped illustrate several aspects of the plotted data. Minimum temperatures tended to occur during the 5th week of the year (early February); maximum temperatures occurred during the 31st week (mid-August). Winter temperatures were characterized by greater week-to-week variability than summer temperatures. In general, the fitted curve consistently overestimated winter temperatures. This trend arose from an apparent asymmetry of the minimum and maximum temperatures about the yearly mean. That

TABLE 1.—Landings of pink shrimp in North Carolina compared with various combinations of winter water temperature data collected at Pivers Island, N.C., and air temperature and rainfall data collected at Morehead City, N.C. Air temperature biweekly periods corresponded with the coldest two consecutive weeks used for water temperature.

Year	Landings Feb.-July (kg, heads off)	Average water temperature (°C)				Average coldest biweekly air temp. (°C)	Total rainfall (cm, Dec.-Feb.)
		Dec.-Mar.	Jan.-Feb.	Coldest week	Coldest two consecutive weeks		
1962	365,390	8.5	8.1	6.2	7.0	8.5	20.3
1963	70,237	7.5	7.0	5.9	6.0	5.5	34.4
1964	274,298	8.1	8.3	6.1	6.2	3.2	39.7
1965	452,246	9.9	9.7	7.1	8.4	—	18.0
1966	150,080	9.0	8.2	4.3	5.2	2.9	27.2
1967	387,773	9.0	8.9	6.9	7.6	8.9	33.7
1968	266,781	—	—	—	—	—	27.7
1969	321,693	—	—	—	—	—	21.2
1970	91,968	—	—	—	—	—	32.8
1971	353,767	—	—	—	—	—	31.7
1972	205,667	—	—	—	—	—	41.1
1973	330,455	9.7	8.7	4.7	5.6	3.6	35.5
1974	518,670	12.1	12.6	7.9	9.1	8.8	49.3
1975	497,163	11.6	11.6	10.2	10.6	8.4	34.7
1976	367,671	10.6	9.6	6.0	7.6	4.4	26.7
1977	13,272	6.4	4.9	2.8	3.1	1.0	28.2
1978	15,567	6.9	6.2	3.5	3.8	4.6	37.8
1979	293,432	8.8	7.6	5.6	5.6	3.8	47.6
1980	157,781	8.4	8.2	3.8	4.8	4.8	29.9
1981	134,626	7.8	7.0	3.7	4.9	2.8	36.7
r^2		0.790	0.804	0.720	0.822	0.50	0.003

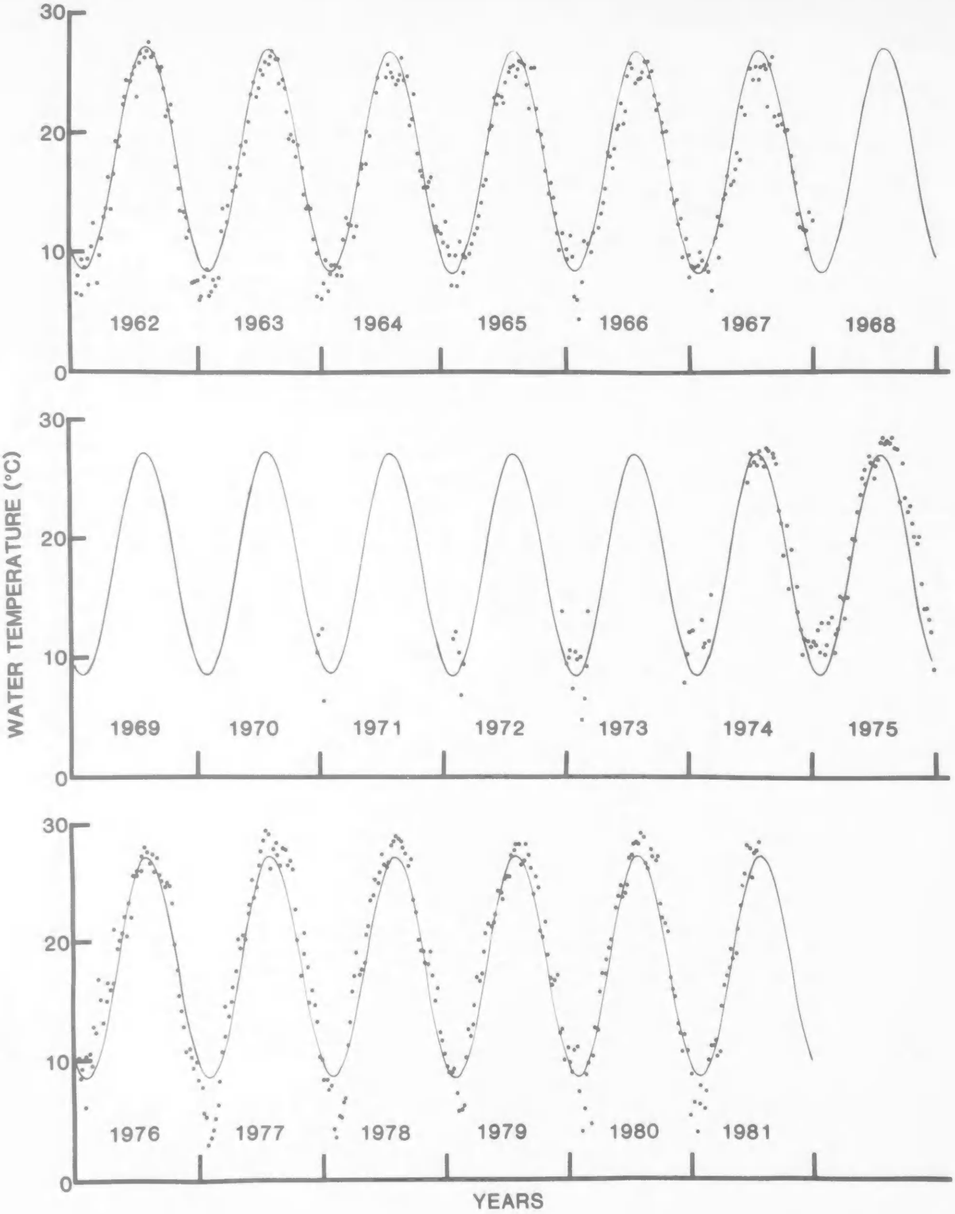


FIGURE 2.—Newport River estuary (Pivers Island) weekly mean water temperatures. Fitted line represents the least squares determined equation: $T_W = a + b_1 \sin\left(\frac{2\pi W}{52}\right) + b_2 \cos\left(\frac{2\pi W}{52}\right)$, where T_W is the mean weekly temperature for week W, $a = 17.88$, $b_1 = -5.20$, and $b_2 = -7.94$ ($R^2 = 0.93$).

is, winter lows were displaced farther from the mean than were summer highs.

As a group the years 1962-67 were cooler in the summer and warmer in the winter than 1974-81. Lower temperatures during cold months reflected a series of very cold winters in the mid-1970s (Diaz and Quayle 1980). An analysis of covariance showed that the average yearly temperature of the 1962-67 year group was significantly different ($P<0.05$) from the 1974-81 group. Either a systematic calibration bias was introduced by different observers, thermographs, and recording locations, or temperatures were actually more extreme in the latter year group. Calibration bias does not satisfactorily explain how both high and low temperature extremes could occur, but a climate phenomenon can be cited. According to R. G. Quayle, NOAA National Climatic Center, Asheville, N.C., the 1962-67 winters were less variable in daily temperature means than the 1973-81 winters. For example, the January and February monthly mean air temperatures at Wilmington, N.C., and Cape Hatteras, N.C., were not different between the two year-groups, but the standard deviations of the monthly means were significantly different at both stations between year-groups (Table 2). Thus, our recorded depressions in weekly winter temperatures in the 1973-81 group probably reflect more extreme actual fluctuations.

TABLE 2.—Comparison of means and standard deviations of January and February air temperatures at two North Carolina coastal stations for year-groups 1962-67 and 1973-81.

Year-group	Air temperature (°C)			
	Wilmington		Cape Hatteras	
	$\bar{x}$	SD	$\bar{x}$	SD
1962-67				
Jan.	7.67	1.51	7.56	1.17
Feb.	8.44	1.73	7.06	1.16
1973-81				
Jan.	7.94	3.74	7.61	3.26
Feb.	8.00	3.10	6.83	3.20

Air-Water Temperature Relation

Close thermal coupling between air and water has been found in shallow estuaries. Roelofs and Bumpus (1953) reported that water temperature in Pamlico Sound showed a seasonal cycle closely related to air temperature. Lindner and Anderson (1956), documenting a winter kill of white shrimp in south Atlantic and Gulf of Mexico waters of the United States, also referred to a close relationship between air temperature and surface water temperature. Smith and Kierspe (1981) presented a model of air-water heat exchanges in a shallow estuary and suggested that their model could reduce the need for in situ instrumentation while providing for close approximation of daily average temperatures.

For the purpose of using air temperatures as proxy data for missing water temperatures (1968-72, Table 1), we decided to examine the relation between local air and water temperatures (Fig. 3). Although air temperature fluctuations were accompanied by a predictable shift in water temperatures over the entire range ($r^2 = 0.97$), at water temperatures below 12°C the relationship was not as useful ($r^2 = 0.68$). We believe that water temperatures rather than air temperatures are required for acceptable predictions of fishery yields in estuaries.

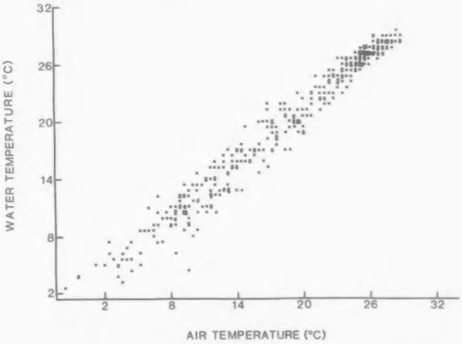


FIGURE 3.—Correlation of Morehead City, N.C., average weekly air temperatures with Newport River estuary (Pivers Island) average weekly water temperatures over 339 consecutive weeks from 1974 to 1981. (Intercept = 2.21, slope = 0.96, $r^2 = 0.97$.) For points below a water temperature of 12°C, $r^2 = 0.68$; and this relationship is not considered useful for predictive purposes during winter.

Relationship Between Temperature, Rainfall, and Pink Shrimp Landings

The February through July pink shrimp landings were considered a dependent variable to be plotted against various combinations of winter temperature data (Table 1). Landings were regressed on average winter water temperature from December through March ($r^2 = 0.79$), average temperature in January and February ($r^2 = 0.80$), average temperature of the coldest week

($r^2 = 0.72$), and average temperature of the two coldest consecutive weeks ($r^2 = 0.82$). All relationships were significant ($P<0.01$). If the average temperature of the two coldest consecutive weeks was <6°C, then shrimp landings were below average (Fig. 4).

Although average winter temperatures (December-March) and average monthly temperatures (January plus February) each accounted for significant portions of the variance in annual landings, the strongest relationship was found between landings and the average of the two coldest consecutive weeks. This may arise because, as Williams (1969b) stated, averages do not adequately represent extremes since they dampen the duration and intensity of the cold. Using a process of expressing temperature in heating degree days, Williams (1969b) postulated that the catch of all species of penaeid shrimps of a given year in North Carolina may depend on net heating degree days during the coldest preceding 6 mo (November-April). He found the poorest catches in cold years (1958, 1961, and 1963) for all three species combined and further suggested that warm years may be as beneficial as cold years are deleterious.

The role of temperature on activity and osmoregulation of pink shrimp has been documented (Williams 1955a, 1960). The lower temperature for activity under experimental conditions was about 14°-16°C; complete cessation of activity was noted below about 10°C. Below 8.8°C, osmoregulatory ability was impaired. Pink shrimp may survive periods of winter cold by burying deeply into the substrate, and Fuss and Ogren (1966) reported that below 14°C, shrimp remain buried, abandoning the usual pattern of nocturnal emergence. Laboratory experiments showed pink shrimp to be more tolerant to combinations of low salinity and low temperature than brown shrimp, and this may explain the occurrence of pink shrimp in North Carolina estuaries during the winter (Williams 1960). In contrast, fall and midwinter brown shrimp immigrants do not survive cold weather as well. The usual recruitment period for brown shrimp postlarvae is February and March; for white shrimp it is June through September (Williams 1965).

Because osmoregulation is impaired at low temperatures, we considered that low salinity could increase mortality caused by low temperatures. Although salinity records were not available, we compared local rainfall measurements with pink shrimp landings from 1962 to 1981. We found no correlation between rainfall and landings ($r^2 = 0.003$) (Table 1). Further, rainfall added no significant contribution to the explanation of variance in landings data when it was included with temperature as a predictive variable (multiple $R^2 = 0.826$). Both the driest (18.0 cm in 1965) and wettest (49.3 cm in 1974) winters occurred in years when landings were very large, approximately 500 metric tons. Williams (1969a) also found no significant relationship between rainfall and total catch of all shrimp species. However, Hunt et al.[3] reported that salinities ≥10‰ and temperatures ≥20°C during April and May are necessary for good brown shrimp harvests in North Carolina. Similarly, Gunter and Hildebrand (1954) found a strong correlation of total rainfall and white shrimp catch in Texas.

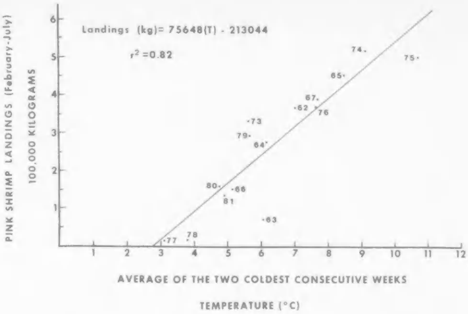


FIGURE 4.—Relation of pink shrimp landings in North Carolina to the average water temperature of the two coldest consecutive weeks in the Newport River estuary. Numbers by dots represent year of landings. (Actual landings of 198,000 kg were predicted to be 165,200 kg, based on the coldest average biweekly period temperature in 1982 of 5.0°C.)

Deviations from the shrimp landings-temperature relationship may, in part, be due to the process of estimating landings. Errors may include improper species identification by fish dealers, lack of accuracy in estimated weight landed, and incomplete landing coverage. The direct trading of shrimp to private individuals by numerous part-time fishermen, plus the recreational landings, neither of which is reported, undoubtedly causes an underestimate of total landings (Caillouet and Koi 1980). On the other hand, because of increased demand and higher prices for shrimp, fishing effort is probably more intensive in recent years. We did not consider effort in our analysis because reliable data were not available. Williams (1969b) concluded that pounds landed almost paralleled his calculated catch-effort index and therefore that actual harvest data satisfactorily represented annual productivity independent of effort. Another source of variability to be considered, the annual variation in the recruitment of postlarvae, was dismissed because Williams (1969b) and Williams and Deubler (1968) found no relation between densities of penaeid shrimp postlarvae and subsequent landings. Similarly Lindner and Anderson (1956) found that a severe cold kill of adult white shrimp in 1940 had no effect on the next year's landings.

---

[3] Hunt, J. H., R. J. Carroll, V. Chinchilli, and D. Frankenberg. 1980. Relationship between environmental factors and brown shrimp production in Pamlico Sound, North Carolina. N.C. Dep. Nat. Resour. Community Dev. Div. Mar. Fish. Spec. Sci. Rep. 33, 29 p.

A number of complications in relating catch and climate were listed by Austin and Ingham (1979). In our study, which began with a conceptual model of an organism and its relation to a physical parameter, some of the following suggested complications were mitigated: 1) A causal relationship of temperature to production was biologically appropriate, because the life history and temperature tolerance of pink shrimp are known; 2) the use of proxy data (air temperature instead of water temperature) was avoided; 3) major variations in the shrimp landings are probably due to cold kill of overwintering shrimp caused by cold-water temperatures ($r^2 = 0.82$); 4) while the quality of the biological data (landings) cannot be judged, the length of the time series (15 yr) is probably adequate; 5) an interest does exist among fishery biologists and managers in using environmental data and relationships for predictive, explanatory, or modeling purposes; 6) although environmental data were point source, landings were from a geographical area (<100 km radius) sufficiently restricted so as not to have masked biota-environmental relations.

ACKNOWLEDGMENTS

We thank Dennis Spitsbergen, North Carolina Division of Marine Fisheries, for information on the distribution of juvenile pink shrimp and on the spring shrimp fishery. Robert Quayle, NOAA National Climatic Center, Asheville, N.C., kindly furnished air temperature data. David Peters, James Waters, William Schaaf, and William Nicholson of the Southeast Fisheries Center Beaufort Laboratory reviewed an earlier revision of the manuscript.

LITERATURE CITED

AUSTIN, H. M., AND M. C. INGHAM.
1979. Use of environmental data in the prediction of marine fisheries abundance. *In* Climate and fisheries: Proceedings from a workshop on the influence of environmental factors on fisheries production, p. 93-98. Center for Ocean Management Studies, University of Rhode Island, Kingston, R.I.

CAILLOUET, C. W., AND D. B. KOI.
1980. Trends in ex-vessel value and size composition of annual landings of brown, pink, and white shrimp from the Gulf and south Atlantic coasts of the United States. Mar. Fish. Rev. 42(12):18-27.

COSTELLO, T. J., AND D. M. ALLEN.
1970. Synopsis of biological data on the pink shrimp *Penaeus duorarum duorarum* Burkenroad, 1939. FAO Fish. Rep. 57:1499-1537.

DIAZ, H. F., AND R. G. QUAYLE.
1980. An analysis of the recent extreme winters in the contiguous United States. Mon. Weather Rev. 108:687-699.

FUSS, C. M., JR., AND L. H. OGREN.
1966. Factors affecting activity and burrowing habits of the pink shrimp, *Penaeus duorarum* Burkenroad. Biol. Bull. (Woods Hole) 130:170-191.

GRADY, J. R.
1971. The distribution of sediment properties and shrimp catch on two shrimping grounds on the continental shelf of the Gulf of Mexico. Proc. Gulf Caribb. Fish. Inst. 23:139-148.

GUNTER, G.
1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas Coast, including the commercial shrimp. Publ. Inst. Mar. Sci., Univ. Tex. 1(2):7-51.
1961. Habitat of juvenile shrimp (family Penaeidae). Ecology 42:598-600.

GUNTER, G., AND H. H. HILDEBRAND.
1951. Destruction of fishes and other organisms on the south Texas coast by the cold wave of January 28 - February 3, 1951. Ecology 32:731-736.
1954. The relation of total rainfall of the state and catch of the marine shrimp (*Penaeus setiferus*) in Texas waters. Bull. Mar. Sci. Gulf Caribb. 4:95-103.

INGHAM, M. C.
1979. Marine environmental conditions off the Atlantic and Gulf coasts of the United States, January 1977-March 1978. Mar. Fish. Rev. 41(5-6):35-47.

KINNE, O.
1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. Oceanogr. Mar. Biol. Annu. Rev. 1:301-340.

LINDNER, M. J., AND W. W. ANDERSON.
1956. Growth, migrations, spawning and size distribution of shrimp *Penaeus setiferus*. U.S. Dep. Inter., Fish Wildl. Serv., Fish. Bull. 56:555-645.

LOUCKS, R. H., AND W. H. SUTCLIFFE, JR.
1978. A simple fish-population model, including environ-

mental influence, for two western Atlantic shelf stocks. J. Fish. Res. Board Can. 35:279-285.

LUNZ, G. R.

1958. Pond cultivation of shrimp in South Carolina. Proc. Gulf Caribb. Fish. Inst. 10:44-48.

NORCROSS, B. L., AND H. M. AUSTIN.

1981. Climate scale environmental factors affecting year class fluctuations of Chesapeake Bay croaker *Micropogonias undulatus*. Va. Inst. Mar. Sci. Spec. Sci. Rep. 110, 78 p.

ROELOFS, E. W., AND D. F. BUMPUS.

1953. The hydrography of Pamlico Sound. Bull. Mar. Sci. Gulf Caribb. 3:181-205.

SMITH, N. P., AND G. H. KIERSPE.

1981. Local energy exchanges in a shallow, coastal lagoon: Winter conditions. Estuarine Coastal Shelf Sci. 13:159-167.

WILLIAMS, A. B.

1955a. A contribution to the life histories of commercial shrimps (*Penaeidae*) in North Carolina. Bull. Mar. Sci. Gulf Caribb. 5:116-146.

1955b. A survey of North Carolina shrimp nursery grounds. J. Elisha Mitchell Sci. Soc. 71:200-207.

1958. Substrates as a factor in shrimp distribution. Limnol. Oceanogr. 3:283-290.

1960. The influence of temperature on osmotic regulation in two species of estuarine shrimps (*Penaeus*). Biol. Bull. (Woods Hole) 119:560-571.

1965. Marine decapod crustaceans of the Carolinas. U.S. Fish Wildl. Serv., Fish. Bull. 65:1-298.

1969a. Penaeid shrimp catch and heat summation, an apparent relationship. FAO Fish. Rep. 57:643-656.

1969b. A ten-year study of meroplankton in North Carolina estuaries: Cycles of occurrence among penaeidean shrimps. Chesapeake Sci. 10:36-47.

WILLIAMS, A. B., AND E. E. DEUBLER.

1968. A ten-year study of meroplankton in North Carolina estuaries: Assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesapeake Sci. 9:27-41.

SEASONAL ABUNDANCE, COMPOSITION, AND PRODUCTIVITY OF THE LITTORAL FISH ASSEMBLAGE IN UPPER NEWPORT BAY, CALIFORNIA

LARRY G. ALLEN[1]

ABSTRACT

This study was designed to characterize the littoral fish populations by 1) composition and principal species, 2) diversity and seasonal dynamics, 3) productivity, and 4) important environmental factors.

Monthly samples (January 1978 to January 1979) obtained with four quantitative sampling methods at three stations in upper Newport Bay yielded 55,561 fishes from 32 species which weighed 103.5 kg. The top five species made up over 98% of the total number of individuals. One species, *Atherinops affinis*, predominated in numbers (76.7% of all fishes) and biomass (79.8%). This dominance was reflected in the low overall H' diversity values for numbers ($H'_N = 0.89$) and biomass ($H'_B = 0.84$). Number of species, number of individuals, and biomass were greatest during the spring and summer.

Quantitative clustering of species based on individual samples revealed five species groups which reflected both microhabitat and seasonal differences in the littoral ichthyofauna. Species Group I was made up of five resident species—*A. affinis, Fundulus parvipinnis, Clevelandia ios, Gillichthys mirabilis*, and *Gambusia affinis*. Species Groups II-VI were composed of summer and winter periodics and rare species.

The mean annual production (9.35 g dry weight/m^2 determined by the Ricker production model) of the littoral zone fishes was among the highest of reported values for comparable studies. This high annual production was mainly the result of the rapid growth of large numbers of juveniles that utilized the littoral zone as a nursery ground. Young-of-the-year *Atherinops affinis* contributed 85% of this total production.

Canonical correlation analysis indicated that temperature and salinity together may influence littoral fish abundance. These two abiotic factors accounted for 83% of the variation in the abundances of individual species. Emigration from the littoral zone, therefore, seems to be cued by seasonal fluctuations in temperature and salinity. I propose that this offshore movement forms an important energy link between the highly productive littoral zone and local, nearshore marine environment.

Semienclosed bays and estuaries are among the most productive areas on Earth, ranking with oceanic regions of upwelling, African savannas, coral reefs, and kelp beds (Haedrich and Hall 1976) in terms of animal tissue produced per year. Bays and estuaries harbor large stocks of nearshore fishes and are important feeding and nursery grounds for many species of fish, including commercially important ones. However, the high productivity of fishes is accompanied by low diversity (Allen and Horn 1975) which probably reflects the stressful ecological conditions in bays and estuaries and the high physiological cost of adaptation to them (Haedrich and Hall 1976). The few studies that have dealt with productivity in estuarine fishes were summarized by Wiley et al. (1972) and Adams (1976b).

Utilization of temperate embayments by juvenile and adult fishes is markedly seasonal with high abundances corresponding to the warmer, highly productive months of spring through autumn. Seasonal species typically spend one spring-autumn period in the shallows of a bay growing at an accelerated rate in the warm, highly productive waters (Cronin and Mansueti 1971).

Most studies to date dealing with composition and temporal changes of bay-estuarine fish populations have been conducted on the Gulf of Mexico and Atlantic coasts of the United States where estuaries are larger and more numerous than those on the Pacific coast (e.g., Bechtel and Copeland 1970; Dahlberg and Odum 1970; Derickson and Price 1973; McErlean et al. 1973; Oviatt and Nixon 1973; Recksiek and McCleave

---

[1] Department of Biological Sciences, University of Southern California, Los Angeles, Calif.; present address: Department of Biology, California State University, Northridge, CA 91330.

Manuscript accepted March 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

1973; Haedrich and Haedrich 1974; Targett and McCleave 1974; Livingston 1976; Moore 1978; Shenker and Dean 1979; Orth and Heck 1980). Although quantitative in nature, many of these investigations suffer from the inefficient (Kjelson and Johnson 1978) trawl sampling gear used and the high mobility of most fishes. Adams (1976a, b) used dropnet samples to accurately assess the density and productivity of the fishes of two North Carolina eelgrass beds. Weinstein et al. (1980) used a combination of block nets, seines, and rotenone collections to derive accurate quantitative estimates of fishes in shallow marsh habitats in the Cape Fear River Estuary, N.C.

Previous investigations of fishes in Newport Bay have included a species list (Frey et al. 1970), a general species account (Bane 1968), two individual species accounts (Fronk 1969; Bane and Robinson 1970), and two studies on the population ecology of the fauna based on juveniles and adults (Posejpal 1969; Allen 1976). An assessment of the ichthyoplankton and demersal fish populations during 1974-75 (Allen and White in press) is the most comprehensive work to date. Despite these studies, a substantial component of the ichthyofauna, the littoral fishes of the upper bay (0-2 m depth from mean higher high water), had not been adequately sampled. In a study of the demersal ichthyofauna of Newport Bay during 1974-75 (Allen 1976), I found that three—*Atherinops affinis*, *Fundulus parvipinnis*, and *Cymatogaster aggregata*—of the five most numerous species were the ones that occurred in the shallow water over the mudflats which cover about 60-70% of the surface area of the upper bay reserve. Despite their high numerical ranking, the relative abundances of these littoral species were underestimated because sampling was carried out almost exclusively by otter trawls in the deeper channels of the upper bay. The recognition of this gap in our knowledge served as the impetus for the present study.

The main purposes of this study were to characterize the littoral ichthyofauna of upper Newport Bay quantitatively by 1) composition and principal species, 2) diversity and seasonal dynamics, 3) productivity, and 4) key environmental factors that are influencing this fish assemblage.

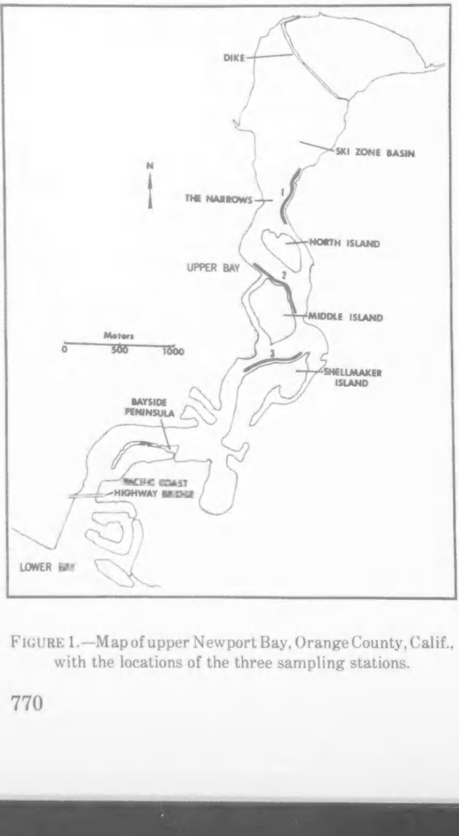


FIGURE 1.—Map of upper Newport Bay, Orange County, Calif., with the locations of the three sampling stations.

METHODS AND MATERIALS

Study Area

Newport Bay (lat. 33°37′30″N, long. 117° 54′ 20″W) is located in Orange County, Calif., 56 km southeast of Los Angeles and 140 km north of the Mexican border (Fig. 1). The upper portion is the only large, relatively unaltered bay-estuarine habitat in California south of Morro Bay (lat. 34.5°N). The low to moderately polluted lower portion, commonly called Newport Harbor, has been severely altered by dredging activities, landfills, and bulkheads to accommodate more than 9,000 boats. The study area, the upper two-thirds of the upper bay, is bordered almost completely by marsh vegetation and mudflats. The California Department of Fish and Game purchased and set aside this area as an ecological reserve in 1975.

Three stations, about 0.5 km in length, were spaced evenly along the shore of the upper Newport Bay (Fig. 1). Sampling was stratified based on prior information on the uniqueness of the fish fauna of the three areas (Allen 1976). This design also allowed thorough coverage of the study area. Each station was situated on a littoral (intertidal) mudflat area adjacent to marsh vegetation and was divided into 10 numbered sections of equal size. Selection of the section sampled each month was random in order to satisfy statistical assumptions and minimize the impact of sampling on any particular section from month to month. Each station included a tidal creek or pool (panne) which was sampled on the marsh islands.

Sampling Procedures

Monthly samples were taken at the three stations during the 13-mo period from January 1978 to January 1979 for a total of 39 station samples. Sampling was carried out within ±3 h of daytime neap high tide to minimize tidal level effects. Two days were usually required to sample three stations, stations 1 and 2 the first day and station 3 the second.

Four types of sampling gear were employed at each station as follows:

1) A 15.2 m × 1.8 m bag seine (BS) with 6.4 mm mesh in the wings and 3.2 mm mesh in the 1.8 × 1.8 × 1.8 m bag was used twice at each station. Hauls were made by setting the net parallel to and 15 m off the shore at a depth of 1-2 m. The BS was then hauled to shore using 15 m polypropylene lines attached to 1.8 m brails on each end of the net. Each haul sampled an area of 220 m^2.

2) A 4.6 m × 1.2 m small seine (SS) with 3.2 mm mesh was pulled 10 m along and 2 m from the shore (at a depth to 1 m) and pivoted to shore. Two hauls were made in the inshore area and one haul in the panne at each station. Each haul sampled an area of 62.4 m^2. [One exception to the sampling routine occurred at station 3 panne in April 1978 when no sample was taken due to a dry panne.]

3) A 2.45 × 2.45 × 1.0 m dropnet (DN) with 3.2 mm mesh was used to sample the water column and bottom at 0.5-1.5 m depth. The DN was suspended from a 5.0 × 5.0 × 1.0 m aluminum pipe frame, released by pins at each corner. Two 19 l plastic buckets were attached to each corner of the frame for flotation. The net and frame were maneuvered into position, anchored, and left undisturbed for 10 min. After release the DN was pursed by the chain line and hauled to shore by nylon line. The DN sampled an area of 6.0 m^2.

4) A small, square enclosure (SE) was used in conjunction with an anesthetic (quinaldine mixed 1:5 with isopropyl alcohol) with the intent of sampling small burrow inhabiting fishes, especially gobies. The SE was constructed of heavy duck material mounted on a 1.0 × 1.0 × 1.0 m collapsible frame of 25.0 mm PVC pipe and sampled 1.0 m^2 of bottom. The SE was set at three randomly chosen positions in an undisturbed portion of each station section at a depth of 0.5-1.0 m. The bottom of the SE was forced into the upper few centimeters of substrate and the quinaldine mixture added to the enclosed water column. The enclosed volume and shallow substrate was then thoroughly searched for 10 min using a long-handled dip net of 1.0 mm mesh.

A detailed comparison of the effectiveness of these four methods is the subject of a separate paper (Horn and Allen[2]).

Ten samples were taken at each of the three stations each month (2 BS samples, 3 SS samples, 2 DN samples, 3 SE samples) for a total of 30 samples/mo and 289 samples over the study (minus one SS haul in April 1978 at station 3).

Catches were either frozen on Dry Ice[3] or preserved in 10% buffered Formalin. Specimens >150 mm SL were injected abdominally with 10% buffered Formalin. Subsamples of frozen specimens were oven dried (40°C) for 48-72 h for dry weight determination. Mean dry weights were based on a minimum of 20 individuals/size-class of each common species at each station each month.

Data on six abiotic factors were recorded or determined for each station: temperature, salinity, dissolved oxygen, sediment particle size, depth of capture (by individual samples), and distance into the upper Newport Bay from the Highway 1 bridge (see Fig. 1).

Production Estimation

Production is the total amount of tissue produced during any given time interval including that of individuals which do not survive to the end of that time interval (Ivlev 1966). Productivity is the rate of production of biomass per unit of time (Wiley et al. 1972). Production of a fish stock is the product of the density of fish and the growth of the individuals (Ricker 1946).

---

[2] Horn, M. H., and L. G. Allen. Comparison of methods for sampling shallow-water estuarine fish populations. Manuscr. in prep. California State University, Fullerton, Fullerton, CA 92634.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

An HP9100A program was developed with the aid of Joel Weintraub (California State University, Fullerton) to calculate the production of each recognizable size-class of the common species, those which were collected in at least 2 consecutive months at each station. The model used was that proposed by Ricker (1946) and modified by Allen (1950) and is calculated as follows:

$$P = G\overline{B}$$

where $G = \dfrac{\log_e \overline{w}_2 - \log_e \overline{w}_1}{\Delta t}$ is the instantaneous coefficient of growth;

$\overline{B} = \dfrac{B_1(e^{G-Z}-1)}{G-Z}$ is the average biomass over the time interval;

$Z = \dfrac{-(\log_e N_2 - \log_e N_1)}{\Delta t}$ is the instantaneous coefficient of population change of the immediate sampling area (station) attributable to mortality and migration;

B is the biomass density of fishes at t_1; w_1, w_2 are the mean weights of individuals at time t_1 and t_2; and N_1, N_2 are the numbers of fishes present at t_1 and t_2. $G-Z$ is the net rate of increase in biomass during Δt (1 mo).

The model assumes that production data need not be corrected for immigration and emigration of fishes in and out of the sampling area, provided the density and growth by size-class are estimated frequently enough to accurately assess the abundance and growth of fishes actually in the sampling area (Chapman 1968).

In the present study, growth increments were estimated from length-frequency data for fishes from all three stations each month for each size-class. The length data, therefore, were representative of the entire population of the size-class in the upper Newport Bay and served to minimize the effects which localized movements into and out of a particular station have on monthly growth values. The average weight, $\overline{w}$, of a size-class per month was calculated as follows: 1) Dry weight equivalent for the median length in a size interval (5 mm intervals) was determined using standard length to dry weight curves for each common species; 2) the proportion (range 0-1) of individuals represented in the size interval was multiplied by the dry weight equivalent for the interval; 3) the products were then summed for all size intervals contained within the particular size-class of the species yielding an average weight, $\overline{w}$. This method proved to be more accurate than simply taking the mean length of the entire size-class and determining the dry weight equivalent.

The "best estimate" of biomass density (B) for each discernible size-class was determined in the following manner: 1) The biomass density (wet weight) derived from the method (BS, SS, DN, or SE) shown to be most effective at sampling the particular species was used. Table 1 lists the species with corresponding collecting gear ranked by their effectiveness at capturing the species. This list is based on a comparative study of the sampling methods (Horn and Allen footnote 2); 2) if, as in a few cases, the biomass estimated was inordinately high, due to a large catch in one replicate sample, the estimate defaulted to the next gear type in the rank order; 3) the biomass estimate in wet weight was converted to a dry weight (DW) equivalent by a conversion factor determined for each species and entered into the production model as B_1 (g DW/m^2). Production is the total of all positive values for size-classes during a time period (1 mo in this case) at each station. Negative values were due to sampling error and emigration and were not included in production estimates.

Large individuals (>100 mm SL) of *Mugil cephalus* were not included in production esti-

TABLE 1.—Methods for best estimate of species densities ranked by effectiveness (Horn and Allen text footnote 2). BS = bag seine; SS = small seine; DN = dropnet; SE = square enclosure.

Species	Methods ranked by effectiveness
Atherinops affinis	BS, SS
Fundulus parvipinnis	SS, BS
Clevelandia ios	SE, SS, DN
Anchoa compressa	BS, SS, DN
Gambusia affinis	SS, BS
Cymatogaster aggregata	BS, DN, SS
Gillichthys mirabilis	SS, SE, BS
Anchoa delicatissima	BS, SS
Mugil cephalus	SS, BS
Engraulis mordax	BS, SS
Leuresthes tenuis	BS, SS
Quietula ycauda	DN, SS
Ilypnus gilberti	DN, SS
Syngnathus spp.	SS, DN
Hypsopsetta guttulata	SS, DN
Lepomis macrochirus	BS, SS
Lepomis cyanellus	BS, SS
All other species	BS, SS

mates because quantitative estimates of densities could not be obtained for the large members of this mobile species.

Data Analysis

Cumulative Species Curve

The cumulative number of species in February (low fish density) and June (high fish density) was plotted against the number of samples taken in order to assess the adequacy of sampling. Two random sequences were used for the arrangement of the 30 samples taken each month by the four methods. Each method sampled a unique subhabitat within the littoral zone. Cumulative species curves (reflecting presence/absence) were based on a combination of methods to insure that all possible species occupying the littoral zone at a particular time were represented.

Diversity

Both the Shannon-Wiener information function (Shannon and Weaver 1949) and species richness were used as measures of diversity for pooled station and upper bay samples. The Shannon-Wiener index reflects both species richness and evenness in a sample.

Cluster Analysis and Canonical Correlation

The Ecological Analysis Package (EAP) developed by R. W. Smith was used at the University of Southern California Computer Center to determine species associations (cluster analysis), species abundance correlations to abiotic factors (multiple regression subprogram), and possible effects of abiotic factors on individual species abundance (canonical correlation).

The cluster analysis utilized the Bray-Curtis index of dissimilarity (Clifford and Stephenson 1975). This index allowed quantitative clustering without assuming normality in the sampled population. A square-root transformation of species counts was done to counter the tendency of this index to overemphasize dominant species.

Canonical correlation analysis was used to determine whether and to what extent abiotic factors interacted with individual species abundances in the 39 station samples over the study period. Two separate canonical correlation analyses were made: The first run included six abiotic factors—temperature (TEMP), salinity (SAL), dissolved oxygen (DO), distance into the upper bay from the Highway 1 bridge (DSTUPB), average particle size of the sediment (APRTSZ), and depth of capture (DPTHCAP); the second included only temperature and salinity to determine the amount of variation these two factors accounted for alone.

RESULTS

Temperature and Salinity Patterns

Water temperatures of the littoral zone at all three stations increased steadily during the period January-June from 14°-15°C to 26°-28°C (Fig. 2). The temperatures remained high (>25°C) throughout the summer months and then declined gradually until November. Between November and December the temperature dropped sharply at each station. Temperatures in the pannes were generally higher than the tempera-

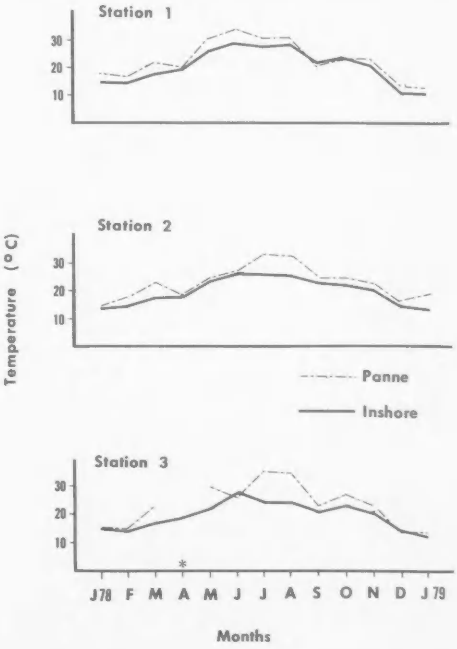


FIGURE 2.—Month-to-month variation (January 1978-January 1979) in water temperature (°C) for the alongshore area and panne at each of the three sampling stations. (* = panne dried-up.)

tures along the shore especially in the summer months (July-September).

Salinity varied more than temperature (Fig. 3) due to rainfall and periodic runoff from surrounding urban areas. In general all stations had low salinities during January through March 1978, a period of heavy rainfall. After May 1978, salinities remained high (between 25 and 32 ppt) with decreases in June 1978 (stations 1 and 3, unknown cause), September 1978 (all stations due to heavy rainfall), and January 1979 (station 3 due to rainfall). Panne salinities at station 1 were consistently low (usually <6 ppt) indicating a constant freshwater input. The pannes at stations 2 and 3, however, usually had salinities equal to or higher than the alongshore area due to evaporation.

Total Catch

Sampling during the 13-mo period yielded 55,561 individuals of 32 species that weighed a total of 103.5 kg (Table 2).

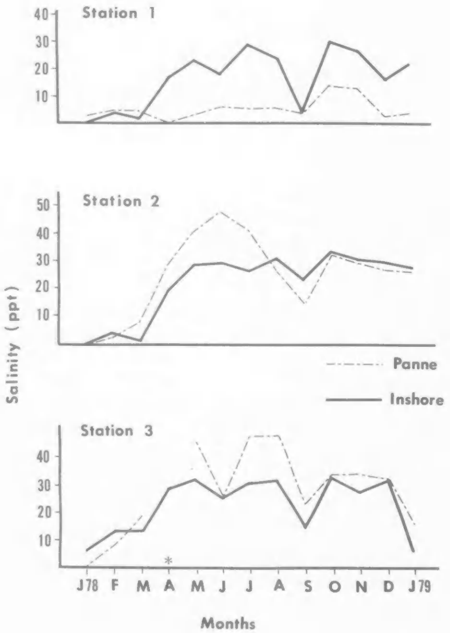


FIGURE 3.—Month-to-month variation (January 1978-January 1979) in salinity (ppt) for the alongshore area and panne at each of the three sampling stations. (* = panne dried-up.)

Atherinops affinis greatly predominated in numbers (76.7%) and biomass (79.9%). *Fundulus parvipinnis* ranked second in both numbers (12.1%) and biomass (7.6%), followed in order by *Gambusia affinis* (5.5% numbers), *Clevelandia ios* (2.4% numbers), and *Anchoa compressa* (1.2% numbers). These five species accounted for 98% of the total number of individuals and 96% of the total biomass (Table 2). The skewed distribution of number of individuals among species was reflected in the relatively low overall H' diversity values of 0.89 for numbers (H'_N) and 0.84 for biomass (H'_B). The vast majority of individuals of most species were either young-of-the-year or juveniles.

Station 1—A total of 13,859 individuals representing 19 species was collected during the year. The catch totaled 22.7 kg. All three of these totals were the lowest of those from the three stations. Overall H' diversity for numbers was 1.17 and for biomass, 0.89. *Atherinops affinis* ranked first in numbers (55.2%) and biomass (76.7%) but was less abundant here than at stations 2 and 3. *Gambusia affinis* (20.6%) and *Fundulus parvipinnis* (19.1%) were common at this station especially in the panne.

Station 2—The greatest number of individuals (24,813) and biomass (42.9 kg) were collected at this site. Although 27 species were captured, over 90% of these individuals were from one species, *Atherinops affinis*. The large number of attached eggs and small (<20 mm) fish caught in July (52% of all *A. affinis*) indicated that this area was a breeding site for *A. affinis*. *Fundulus parvipinnis* (4.4%) was second in numerical rank. H' for numbers (0.49) and biomass (0.70) were low.

Station 3—A total of 16,889 fishes belonging to 23 species were obtained at this station. *Atherinops affinis* made up 74.4% of the individuals and 78.8% of the 37.9 kg total biomass. Other important species in order of decreasing numerical abundance were *Fundulus parvipinnis* (17.6%), *Clevelandia ios* (3.4%), *Cymatogaster aggregata* (1.3%), and *Anchoa compressa* (1.3%). Overall, H'_N and H'_B were 0.87 and 0.85, respectively.

Cumulative Species Curves

Cumulative species curves from February and June (Fig. 4) reached an asymptote before 20 samples (about 66% of total samples), indicating

TABLE 2.—Monthly abundance and biomass for fish species inhabiting the littoral zone of upper Newport Bay totaled for stations 1-3 (January 1978-January 1979).

Species	January 1978		February		March		April		May		June		July	
	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)
Atherinops affinis	15	70.5	5	158.3	4	92.0	15	59.1	322	1,212.1	6,296	2,377.6	19,817	19,093.3
Fundulus parvipinnis	377	315.7	208	198.3	181	90.4	17	20.7	35	92.2	89	112.3	758	854.8
Gambusia affinis	46	10.3	23	7.1	9	3.2	8	2.8	56	7.1	235	107.4	573	342.9
Clevelandia ios	49	21.4	39	14.3	80	12.9	47	6.1	100	22.4	74	15.8	485	109.0
Anchoa compressa	26	82.9	1	1.2	15	29.4	136	629.3	317	4,393.4	98	1,154.6	77	920.5
Cymatogaster aggregata							11	11.5	141	196.8	4	5.7		
Gillichthys mirabilis	12	2.4	38	5.9	14	3.5	5	10.0	17	39.6	49	127.1	52	141.4
Anchoa delicatissima	10	6.5	1	0.2	28	16.8	47	86.7	17	48.2			1	3.0
Mugil cephalus	41	78.0	11	7.1	1	1.5	1	555.5	1	550.0				
Engraulis mordax													81	89.4
Leuresthes tenuis														
Quietula ycauda	1	1.0							3	1.4	9	3.9	28	14.9
Ilypnus gilberti									3	0.5	10	1.0	24	6.5
Lepomis cyanellus			1	5.2										
Syngnathus auliscus									4	3.6	10	8.7	4	3.3
Hypsopsetta guttulata									10	1.9	4	12.9	2	18.2
Lepomis macrochirus	2	8.1	4	22.2	2	4.1								
Syngnathus leptorhynchus							1	2.1			2	2.6		
Leptocottus armatus					1	1.0			2	4.7	1	1.6		
Acanthogobius flavimanus							2	0.5	1	4.0				
Paralichthys californicus													2	5.4
Pimephales promelas			2	0.2										
Morone saxatilis											1	317.1		
Urolophus halleri														
Mustelus californicus													1	58.0
Seriphus politus														
Cynoscion nobilis													1	6.6
Sphyraena argentea														
Girella nigricans													1	0.4
Symphurus atricauda			1	0.2										
Porichthys myriaster														
Umbrina roncador														
Totals	579	596.8	334	420.2	335	254.8	287	1,384.3	1,029	6,577.9	6,882	4,248.3	21,907	21,667.6
n	10		12		10		11		15		14		16	
H'	1.29	1.46	1.33	1.27	1.37	1.55	1.61	1.22	1.76	1.07	0.44	1.24	0.46	0.56

TABLE 2.—*Continued.*

Species	August		September		October		November		December		January 1979		Totals			
	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	% No.	Wt (g)	% Wt
Atherinops affinis	4,645	13,181.2	4,122	9,606.2	2,902	14,016.0	2,474	12,409.8	1,143	5,738.8	831	4,650.1	42,591	76.67	82,665.0	79.86
Fundulus parvipinnis	312	250.1	1,707	2,323.0	1,023	2,638.8	1,356	738.0	593	259.7	66	26.5	6,722	12.10	7,920.5	7.65
Gambusia affinis	252	42.4	1,029	399.4	680	126.2	149	15.2	20	2.1			3,077	5.54	1,066.1	1.03
Clevelandia ios	68	16.4	151	41.8	66	16.3	142	31.3	28	3.9	5	1.1	1,334	2.40	312.7	0.30
Anchoa compressa	7	104.9	3	53.1	4	104.8							684	1.23	7,474.1	7.22
Cymatogaster aggregata	61	390.9	2	16.6			2	34.1	1	22.6	1	12.4	223	0.40	690.6	0.67
Gillichthys mirabilis	4	27.0	1	20.0	4	37.1	1	12.0			6	0.3	203	0.37	426.3	0.41
Anchoa delicatissima	64	234.4	26	71.7	1	3.5							195	0.35	471.0	0.46
Mugil cephalus									68	13.3	9	1.5	132	0.24	1,206.9	1.17
Engraulis mordax			29	58.6	2	7.2					1	—	113	0.20	155.2	0.15
Leuresthes tenuis	85	57.8	3	2.3									88	0.16	60.1	0.06
Quietula ycauda	5	1.9	4	1.5	2	0.4	1	0.1					53	0.10	25.1	0.02
Ilypnus gilberti							1	0.1					38	0.07	8.1	0.01
Lepomis cyanellus			31	49.3									32	0.06	54.5	0.05
Syngnathus auliscus	1	0.4			1	0.1							20	0.04	16.1	0.02
Hypsopsetta guttulata							1	2.9			2	0.2	19	0.03	36.1	0.03
Lepomis macrochirus													8	0.01	34.4	0.03
Syngnathus leptorhynchus	1	2.8	3	5.2							1	0.3	8	0.01	13.0	0.01
Leptocottus armatus													4	0.01	7.3	0.01
Acanthogobius flavimanus													3	0.01	4.5	<0.01
Paralichthys californicus													2	<0.01	5.4	0.01
Pimephales promelas													2	<0.01	0.2	<0.01
Morone saxatilis													1	<0.01	317.1	0.31
Urolophus halleri	1	430.0											1	<0.01	430.0	0.42
Mustelus californicus													1	<0.01	58.0	0.06
Seriphus politus					1	0.3							1	<0.01	0.3	<0.01
Cynoscion nobilis													1	<0.01	6.6	0.01
Sphyraena argentea							1	4.2					1	<0.01	4.2	<0.01
Girella nigricans													1	<0.01	0.4	<0.01
Symphurus atricauda													1	<0.01	0.2	<0.01
Porichthys myriaster							1	0.1					1	<0.01	0.1	<0.01
Umbrina roncador	1	44.2											1	<0.01	44.2	0.04
Totals	5,507	14,784.4	7,111	12,648.7	4,686	16,950.7	4,129	13,247.8	1,853	6,040.4	922	4,692.4	55,561		103,514.3	
n	14		13		11		11		6		9		32			
H'	0.69	0.55	1.10	0.77	0.99	0.54	0.92	0.27	0.90	0.23	0.42	0.06	0.89		0.84	

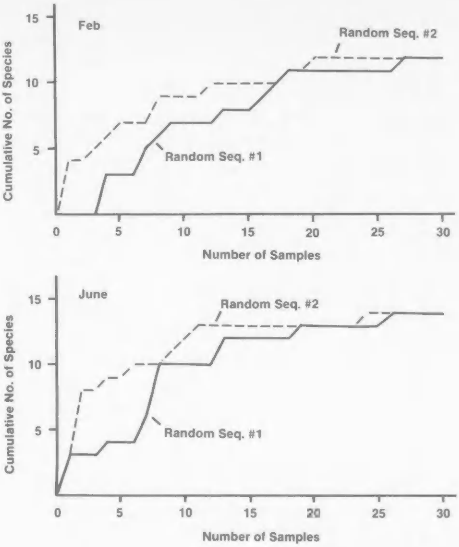


FIGURE 4.—Cumulative number of species as a function of the number of samples of all methods at stations 1-3 combined in upper Newport Bay for two different months (February and June 1978) during the study period. Curves were generated by two random sequences for each month.

that the range of fish species in the area had been adequately sampled by the four methods. Accumulation of species in June, however, was generally more rapid than in February.

Seasonal Abundance and Diversity

Fish abundance and diversity fluctuated markedly during the 13 mo of the study (Fig. 5). As a whole, the ichthyofauna of the littoral zone showed increased species richness from 10 species in January to 16 species in July 1978. The number of species was elevated (>14) for the entire spring-summer period from May to August 1978. Richness then decreased through the fall, reaching its lowest point of six species in December 1978. Diversity H' values fluctuated in a pattern opposite to that of species richness. H'_N decreased during the summer from a high in May of 1.76 to a low in June of 0.44. H'_B also decreased sharply in summer but unlike H'_N continued to decline for the remainder of the study. Both the number of individuals and biomass began to increase dramatically during May 1978 and reached peaks of 21,907 individuals and 21.7 kg in June. Both numbers and biomass decreased in August with number of individuals increasing again in September. Biomass declined once again in September during a period of rainfall and then increased in October. In the months from October 1978 to January 1979 a rapid decline in both numbers and biomass was evident and was especially pronounced from November to December. A greater number of individuals (992-579) and much greater biomass (4,692-597 g) was obtained in January 1979 than in January 1978.

Species Associations

Cluster analysis based on individual samples yielded five species groups which, upon further

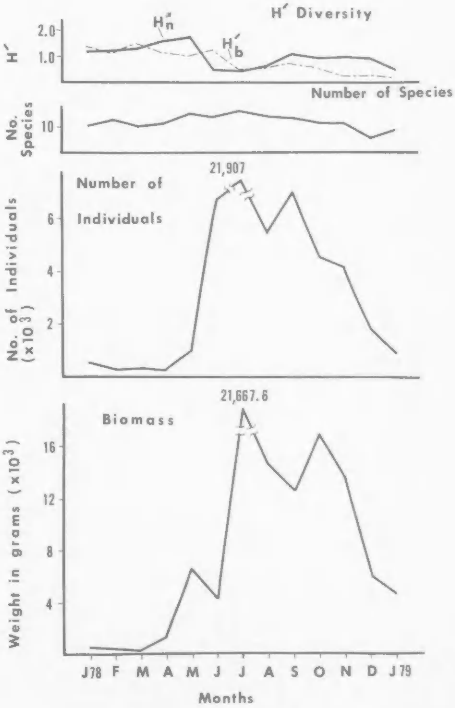


FIGURE 5.—Monthly variation (January 1978-January 1979) in total number of species, diversity H′ (for numbers, H'_N, and biomass, H'_B), number of individuals and biomass (g) for fishes collected by all methods at stations 1-3 combined in the littoral zone of upper Newport Bay.

examination, reflected both spatial (microhabitat) and seasonal differences in the littoral ichthyofauna (Fig. 6).

Group I was a loosely associated group of the five resident species (maintain populations year round in littoral zone) which could be further divided into three subgroups. Subgroup A had only one member, *Atherinops affinis*, an abundant schooling species. *Clevelandia ios* and *Gillichthys mirabilis* which comprised subgroup B are burrow-inhabiting gobiids of the shallows and pannes. Subgroup C included two species, *Fundulus parvipinnis* and *Gambusia affinis*, which inhabited pannes and other high intertidal areas. *Clevelandia ios*, *G. mirabilis*, and *F. parvipinnis* are residents of salt marshes in California and other west coast estuaries and are probably the species most threatened by alterations of these habitats.

Group II consisted of three midwater schooling species—*Anchoa compressa*, *A. delicatissima*, and *Cymatogaster aggregata*—most of which were caught mainly from January to August.

Group III was made up of three distinctly seasonal, benthic species: Two gobiids, *Quietula ycauda* and *Ilypnus gilberti*, and a cottid, *Leptocottus armatus*, which was relatively rare during 1978 compared with previous years (pers. obs.).

Group IV included an engraulid, *Engraulis mordax*; syngnathids, Syngnathus spp. (including *S. auliscus* and *S. leptorhynchus*); and the pleuronectid, *Hypsopsetta guttulata*. These species were seasonally present in mid- to late summer. Members of this group were only loosely associated (> 80% distance).

Group V was composed of four species which were collected at times of low salinities. *Lepomis macrochirus* and juveniles of *Mugil cephalus* were sampled together early in the year (January-March 1978). *Lepomis cyanellus* and *Leuresthes tenuis* were found together only in September.

Group VI included 12 rare species, most of which could be considered summer periodics in the littoral zone in 1978. These were *Umbrina roncador*, *Urolophus halleri*, *Paralichthys californicus*, *Mustelus californicus*, *Cynoscion nobilis*, *Acanthogobius flavimanus*, *Sphyraena argentea*, *Girella nigricans*, *Symphurus atricauda*, *Porichthys myriaster*, *Morone saxatilis*, and *Seriphus politus*.

Members of the species groups identified in the dendrogram (Fig. 6) are illustrated in dia-

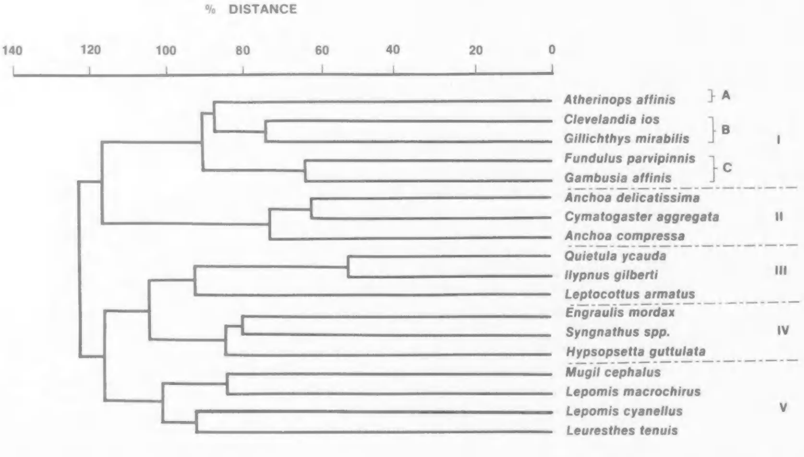


FIGURE 6.—Dendrogram of the clustering of littoral fish species by individual samples taken at stations 1-3 in upper Newport Bay, five species groups (Roman numerals) are recognized according to the Bray-Curtis index of dissimilarity (% distance). A, B, and C are subgroups of species Group I.

grams (Figs. 7-9), depicting occurrences in the alongshore area or panne during three different time periods (January-March 1978, April-September 1978, and October 1978-January 1979). Only species with ≥5 individuals during each time segment were included in the diagrams. These diagrams illustrate the high degree of seasonality within this fish assemblage.

During the January-March 1978 period of heavy rainfall, members of three species groups (I, II, and V) were present in relatively low abundances (Fig. 7). A halocline existed at station 3 during this period, and *Atherinops affinis* was collected only seaward of the halocline at this station. Representatives of group V, *Mugil cephalus* juveniles and *Lepomis macrochirus*, were found associated with very low salinities. Large *M. cephalus* were observed in both the channel and littoral areas during most of the year.

The spring-summer period of April-September 1978 was characterized by increased water temperatures and salinities, accompanied by increased numbers of species and individual fishes (Fig. 8). Green algal beds, composed primarily of *Enteromorpha* sp., *Chaetomorpha linum*, and *Ulva lobata*, developed along the shore of the entire upper bay, and served as a nursery area for large numbers of juvenile fishes. All species groups, except V, were represented during this time. Juveniles of *Atherinops affinis* occurred in large numbers in the shallows with juvenile *Cymatogaster aggregata* also being abundant at station 3. Young-of-the-year *F. parvipinnis* were very abundant in the pannes, especially at stations 1 and 3.

By October the extensive algal beds had disappeared. The October 1978-January 1979 period was marked by decreased number of species and abundance (Fig. 9). The only common species were members of group I (residents) with a few juvenile *M. cephalus* representing group V.

Productivity

Annual production (mean of three stations by month) of the entire upper Newport Bay was 9.35 g DW/m^2 per year (Table 3). Young-of-the-year *Atherinops affinis* contributed 85.1% to total production followed by *Anchoa compressa* (4.9%) and *Fundulus parvipinnis* (4.2%).

Productivity was highly seasonal with the spring-summer period (April-September) accounting for 75.9% of the total annual production (Table 3, Fig. 10). Productivity, which was very

TABLE 3.—Monthly mean production (g DW/m^2) for individual species inhabiting the littoral zone (excluding panne) of upper Newport Bay (February 1978-January 1979).

Species	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Total annual	% total production
Atherinops affinis (adult)				0.0280	0.1049								0.1329	1.42
A. affinis (78 class)					0.0800	0.6764	5.1397		1.2942	0.6428		0.1307	7.9638	85.15
Fundulus parvipinnis	0.0005		0.0007	0.0240	0.0167	0.1323	0.0352	0.0826	0.1033				0.3953	4.23
Clevelandia ios	0.0003			0.0027	0.0051	0.0093	0.0068		0.0431			0.0145	0.0818	0.87
Anchoa compressa	0.0142		0.0045	0.1127	0.2524	0.0485	0.0154		0.0075				0.4552	4.87
Gillichthys mirabilis		0.0001	0.0014		0.0889	0.0361	0.0102	0.0020					0.1387	1.48
Hypsopsetta guttulata					0.0082	0.0020							0.0102	0.11
Mugil cephalus	0.0006	0.0004										0.0003	0.0013	0.01
Anchoa delicatissima	0.0030	0.0002	0.0039	0.0084	0.0013		0.0001	0.0017					0.0186	0.20
Quietula ycauda						0.0011							0.0011	0.01
Engraulis mordax							0.0046	0.0003					0.0049	0.05
Cymatogaster aggregata				0.0074	0.0072	0.0023		0.0101	0.0009				0.0279	0.30
Ilypnus gilberti						0.1197							0.1197	1.28
Lepomis macrochirus	0.0008												0.0008	0.01
Monthly total	0.0194	0.0007	0.0105	0.1832	0.5647	1.0277	5.2120	0.0967	1.4490	0.6428	0	0.1455	9.3522 g DW/m^2/yr	
													April-September 7.0948-75.86%	

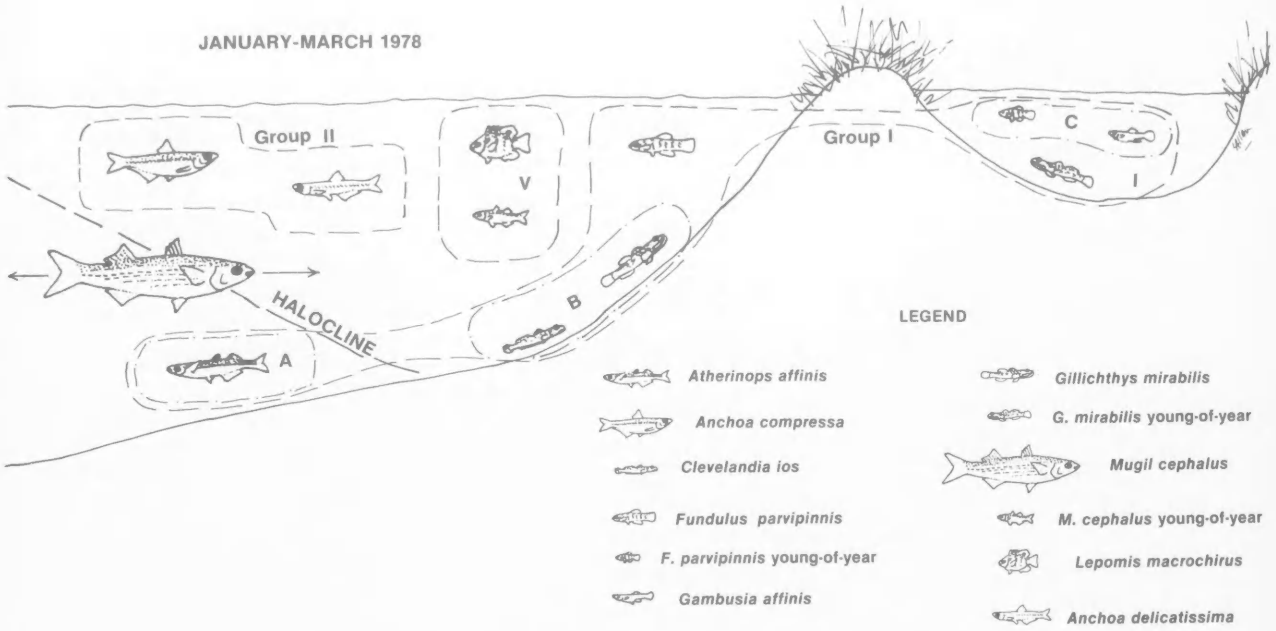

JANUARY-MARCH 1978
Group II
V
Group I
C
I
HALOCLINE
B
A
LEGEND
Atherinops affinis
Anchoa compressa
Clevelandia ios
Fundulus parvipinnis
F. parvipinnis young-of-year
Gambusia affinis
Gillichthys mirabilis
G. mirabilis young-of-year
Mugil cephalus
M. cephalus young-of-year
Lepomis macrochirus
Anchoa delicatissima

FIGURE 7.— Diagrammatic representation of the principal species inhabiting the littoral zone (alongshore and panne) of upper Newport Bay during January-March 1978. Inclusion level for species was ≥5 individuals in the samples during the period. Dashed lines enclose species from groups derived in the dendrogram of Figure 6. Arrows indicate inshore-offshore occurrence.

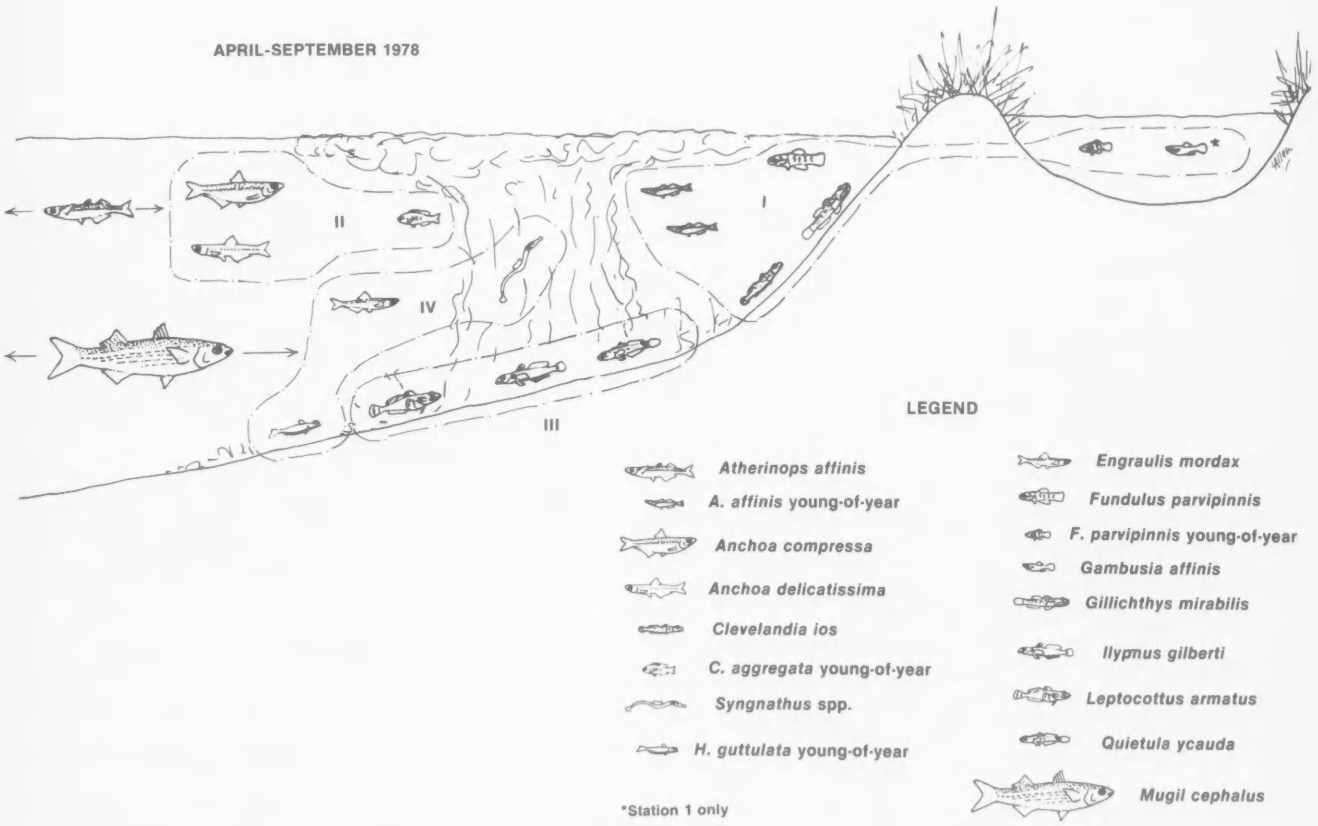

APRIL-SEPTEMBER 1978
I
II
III
IV
*
Allen
LEGEND
Atherinops affinis
A. affinis young-of-year
Anchoa compressa
Anchoa delicatissima
Clevelandia ios
C. aggregata young-of-year
Syngnathus spp.
H. guttulata young-of-year
*Station 1 only
Engraulis mordax
Fundulus parvipinnis
F. parvipinnis young-of-year
Gambusia affinis
Gillichthys mirabilis
Ilypnus gilberti
Leptocottus armatus
Quietula ycauda
Mugil cephalus

FIGURE 8.—Diagrammatic representation of the principal species inhabiting the littoral zone of upper Newport Bay during April-September 1978. Wavy vertical lines represent the large algal beds present during this period. Other information is the same as in Figure 7. (*Syngnathus* spp. includes *S. leptorhynchus* and *S. auliscus*.)

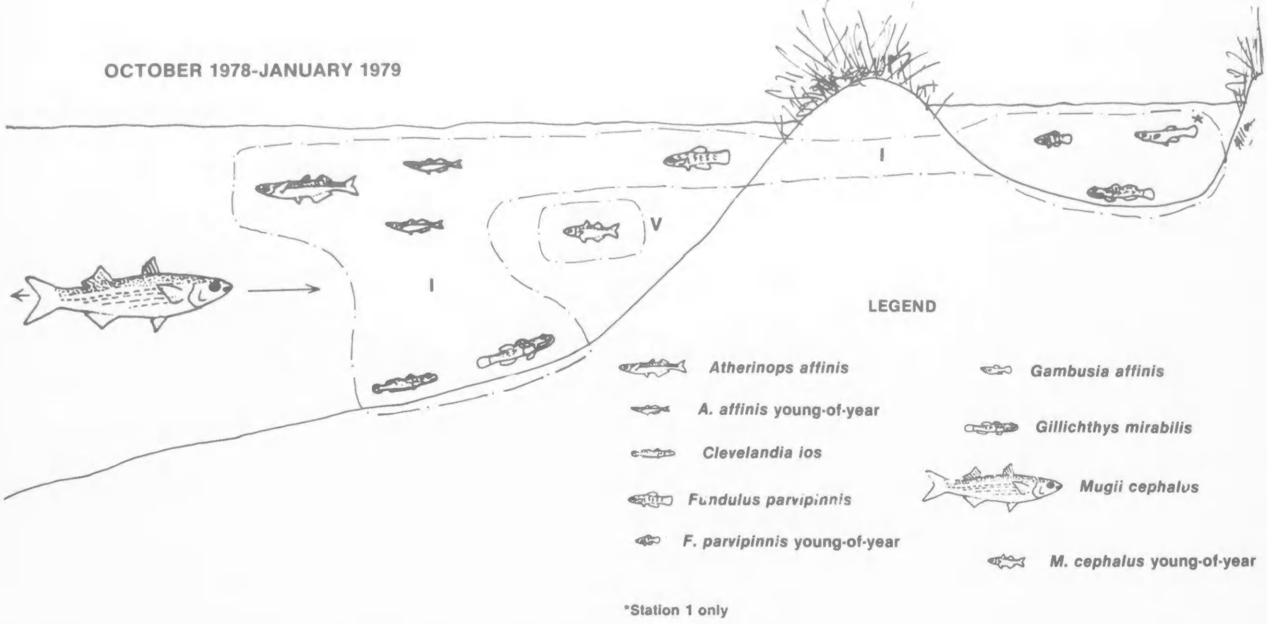

OCTOBER 1978-JANUARY 1979
I
V
I
*
LEGEND
Atherinops affinis
A. affinis young-of-year
Clevelandia ios
Fundulus parvipinnis
F. parvipinnis young-of-year
Gambusia affinis
Gillichthys mirabilis
Mugil cephalus
M. cephalus young-of-year
*Station 1 only

FIGURE 9.—Diagrammatic representation of the principal species inhabiting the littoral zone of upper Newport Bay during October 1978-January 1979. Other information as in Figure 7.

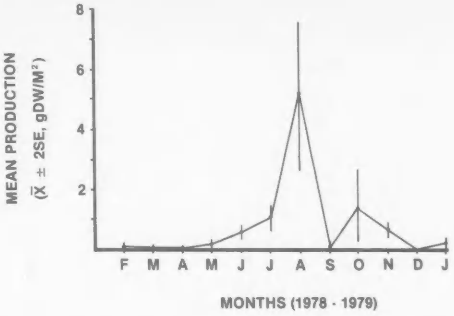


FIGURE 10.—Monthly variation in mean production ($\bar{x} \pm 2$ SE, g DW/m^2) of the littoral fishes from three stations in upper Newport Bay (February 1978-January 1979).

low from February to May 1978, increased rapidly from June to a peak in August (5.2 g DW/m^2). Monthly production then declined drastically in September, a period of heavy rainfall during which many of the larger young-of-the-year *Atherinops affinis* emigrated from the study area. Production increased in October but then showed a steady decline to zero in December, a time of a sharp decrease in mean water temperature in the upper bay.

Relationship of Abiotic Factors to Fish Abundance and Distribution

Temperature was found to have a significant, positive correlation ($P<0.01$, df = 37) with number of species ($r = 0.42$), number of individuals ($r = 0.48$), and biomass ($r = 0.54$) when station totals were considered. Similarly, salinity was significantly correlated with number of individuals ($r = 0.36$) and biomass ($r = 0.64$) (Table 4).

Temperature was the factor which yielded the highest number of significant correlations (6) with individual species, followed by salinity, dissolved oxygen, distance into the upper bay, and depth of capture, each with four (Table 4).

An analysis of intercorrelations among abiotic factors yielded three significant ($P<0.05$, df = 37) positive relationships: 1) Temperature and salinity ($r = 0.48$); 2) temperature and dissolved oxygen ($r = 0.53$); and 3) dissolved oxygen and distance into the upper bay ($r = 0.32$).

According to canonical correlation analysis, the six abiotic variables accounted for 93% of the variation in individual species abundances along the first canonical axis (Table 5). A second run indicated that 83% of the variation in species abundances could be accounted for by temperature and salinity alone. This finding strongly implies that interactive effects of temperature

TABLE 4.—Correlation coefficients (r) of individual species numbers and of total number of species, number of individuals, and biomass with six environmental factors. TEMP = temperature, SAL = salinity, DO = dissolved oxygen, DSTUPB = distance into upper Newport Bay from Highway 1 bridge, APRTSZ = average particle size of sediments, DPTHCAP = depth of capture.

	Abiotic factors					
Species	TEMP	SAL	DO	DSTUPB	APRTSZ	DPTHCAP
Atherinops affinis	0.55**	0.57**	0.21	0.00	−0.12	0.23
Fundulus parvipinnis	0.18	0.15	−0.31*	0.00	−0.06	0.03
Anchoa compressa	0.38*	0.21	0.35*	−0.01	0.05	0.24
Clevelandia ios	0.43**	0.22	0.08	−0.09	−0.16	0.23
Mugil cephalus	−0.62**	−0.29	−0.10	0.11	0.26	0.02
Gillichthys mirabilis	0.25	−0.22	0.44**	0.31*	0.01	0.00
Anchoa delicatissima	0.10	0.08	−0.22	−0.22	0.05	−0.02
Gambusia affinis	0.21	−0.25	0.16	0.58**	−0.07	−0.02
Hypsopsetta guttulata	0.30	0.21	0.43**	0.26	−0.10	0.28
Cymatogaster aggregata	0.14	0.28	−0.01	−0.34*	0.01	0.14
Quietula ycauda	0.46**	0.35*	0.19	−0.16	0.01	0.35*
Ilypnus gilberti	0.39*	0.31*	0.23	−0.10	0.11	0.33*
Lepomis macrochirus	−0.29	−0.44*	−0.23	0.10	0.09	0.04
Lepomis cyanellus	0.06	−0.27	−0.29	0.16	−0.20	0.05
Engraulis mordax	0.22	0.16	0.00	0.13	−0.07	0.33*
Leuresthes tenuis	0.16	0.14	−0.09	−0.15	0.10	−0.01
Leptocottus armatus	0.29	0.13	0.38	−0.09	−0.01	0.05
Syngnathus spp.	0.53	0.23	0.35	0.08	−0.07	0.33*
Species totals (by station)						
No. of species	0.42**	0.05	—	—	—	—
No. of individuals	0.48**	0.36*	—	—	—	—
Biomass	0.54**	0.64**	—	—	—	—

* = significant at 0.05 level.
** = significant at 0.01 level.

TABLE 5.—Summary of two canonical correlation runs of individual species abundances against environmental variables.

Axis	R^2	R	X^2	df
Run No. 1 (6 environmental; 18 species)				
1	0.93	0.96	212.9*	126
2	0.84	0.92	144.1*	102
3	0.73	0.85	96.3	80
Run No. 2 (temperature, salinity only, 18 species)				
1	0.83	0.91	77.8*	36
2	0.61	0.78	26.5	17

* = significant at 0.01.

and salinity were important in influencing species abundance.

The 18 most common species were ordinated along temperature and salinity axes using simple correlation values (r) as an index of relative influence of these two factors (Fig. 11). Thirteen of the 18 species were positioned in the upper right quadrant indicating that they were all positively correlated with temperature and salinity. Three species, *Gambusia affinis, Gillichthys mirabilis,* and *Lepomis cyanellus,* located in the upper left quadrant correlated positively with temperature, but negatively with salinity. The lower left quadrant includes two species, *Lepomis macrochirus* and *Mugil cephalus,* with negative temperature and salinity influences. No species were positioned in the negative temperature, positive salinity quadrant probably because this situation rarely occurred in the littoral zone in 1978.

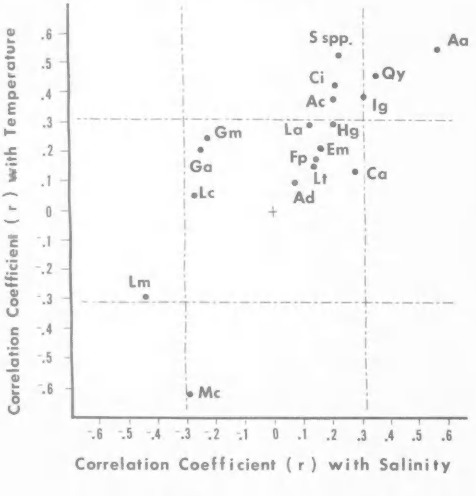


FIGURE 11.—Ordination of 18 common species of the littoral zone of upper Newport Bay on correlation coefficients (r) for temperature (y-axis) and salinity (x-axis). Dashed lines indicate 0.05 significance levels. Aa-*Atherinops affinis*, Ac-*Anchoa compressa*, Ad-*Anchoa delicatissima*, Ca-*Cymatogaster aggregata*, Ci-*Clevelandia ios*, Em-*Engraulis mordax*, Fp-*Fundulus parvipinnis*, Ga-*Gambusia affinis*, Gm-*Gillichthys mirabilis*, Hg-*Hypsopsetta guttulata*, Ig-*Ilypnus gilberti*, La-*Leptocottus armatus*, Lm-*Lepomis macrochirus*, Lt-*Leuresthes tenuis*, Mc-*Mugil cephalus*, Qy-*Quietula ycauda*, Sspp-*Syngnathus* spp.

DISCUSSION

Composition, Diversity, and Seasonal Dynamics

The ichthyofauna of the littoral zone in upper Newport Bay was numerically dominated by a few, low trophic-level species (five species accounted for >98% of all specimens collected), a situation similar to that found in many estuarine fish populations (Allen and Horn 1975). *Atherinops affinis* is an opportunistic feeder and has been characterized as both a herbivore/detritivore (Allen 1980) in upper Newport Bay and a low-level carnivore (Fronk 1969; Quast 1968). The second most abundant fish, *Fundulus parvipinnis,* is a low-level carnivore that feeds on small crustaceans and insects (Allen 1980; Fritz 1975). *Gambusia affinis, Clevelandia ios,* and *Anchoa compressa* are, likewise, low-level carnivores, feeding mainly on insects, benthic microinvertebrates, and zooplankton (Allen 1980).

Large individuals of *Mugil cephalus* were not sampled effectively, but probably constituted a significant proportion of biomass within these fish assemblages. Adult *M. cephalus* fed mainly on detritus and pennate diatoms (Allen 1980). This essentially herbivorous diet closely matches that described by Odum (1970) for *M. cephalus.*

The overall H' diversity values (H'_N range, 0.42-1.76; overall 0.89) for the littoral zone were comparable to values derived from other studies of bay-estuarine fish faunas and to other studies in Newport Bay. Haedrich and Haedrich (1974) derived values of 0.33-1.03 for Mystic River Estuary, Mass.; Stephens et al. (1974) presented indices of 0.65-2.08 for Los Angeles Harbor, Calif.; Allen and Horn (1975) published values of 0.03-1.11 for Colorado Lagoon, Alamitos Bay, Calif.; and Quinn (1980) calculated values of 0.21-2.59 (overall 1.9) for Serpentine Creek in subtropical Queensland. Using otter trawl data, I calculated H'_N values of 0.20-1.96 (overall 0.98) for the upper Newport Bay in 1974-75 (Allen 1976). The concurrent bimonthly portion of this study (Horn and Allen 1981) obtained a bimonthly range for numbers of 0.48-2.17 (overall 1.05) when the deeper channel areas were also sampled. The relatively wide range of H'_N values in all of the above studies reflects the differential utilization of these embayments by fishes on a seasonal basis. At the same time, the low overall diversity reflects dominance both in numbers and biomass by a few species. The seasonal usage has the effect of increasing annual diversity, although only one or two species dominate numerically at any one time. The H' values for biomass (H'_B range 0.23-1.55; overall 0.84) were fairly close to those for numbers and, again, mainly reflected the dominance of *A. affinis* (~80%). In all, 26 of the 32 reported species had young-of-the-year fishes, making up a significant portion of their populations. Fluctuations in juvenile population levels had a substantial effect on the littoral fish populations. Juvenile recruitment plus the immigration of adult fishes presumably for reproduction or for exploitation of high productivity in warmer months were the principal causes for seasonal changes in the ichthyofauna. These activities reflect the widely recognized function of bay-estuarine environments as spawning and nursery grounds (Haedrich and Hall 1976).

The general pattern of increased number of species and numbers of individuals during the late spring through fall period in upper Newport Bay has been observed in many other studies of temperate bay-estuarine fishes (e.g., Pearcy and Richards 1962; Dahlberg and Odum 1970; Allen and Horn 1975; Adams 1976a). Several studies of estuarine fish populations have, in addition, detected summer depressions in abundance between peaks in spring and fall in other estuaries (Livingston 1976; Horn 1980) and in lower Newport Bay (Allen 1976).

Studies of subtropical estuarine fish populations have shown a trend in seasonal abundances that is 6 mo out of phase with the above observations. Fish abundances were highest during the winter months (November-March) in the Huizache-Caimanero Lagoon of Mexico due to increases in members of both demersal and pelagic fishes (Amezcua-Linares 1977; Warburton 1978). This coastal lagoon system is subject to a narrower range of temperatures over the year (18.3°-27.9°C) than most temperate systems. However, the Mexican system undergoes wide variation in salinity, especially during the rainy season from July to October (see section Influence of Abiotic Factors).

Species Associations

Species groupings were subject to strong seasonal influence and bore a striking resemblance to the classification scheme of Atlantic nearshore fish communities proposed by Tyler (1971). According to Tyler's classification the Atlantic nearshore fish communities can be divided into regular and periodic components. Periodic components can be winter seasonals, summer seasonals, or occasionals. The upper Newport Bay fish assemblage had regulars (group I) and periodics (groups II-V). The "anchovy" group (II), the "goby" group (III), and the "*Engraulis-Hypsopsetta*" group (IV) were all summer seasonals. Group V had both winter seasonals in *Mugil cephalus* and *Lepomis macrochirus* and summer seasonals in *Lepomis cyanellus* and *Leuresthes tenuis*. The latter group, however, could best be characterized by the affinity of its components to lower salinities rather than to a particular time of year. The occasional component was represented by the 12 species of group VI which also occurred in the summer. Thus Tyler's classification may have a broader application than he originally proposed, and perhaps holds true for many estuarine ichthyofaunas.

Species Densities and Productivity

Density estimates for some species of littoral fishes are particularly difficult to obtain. Such species include small, burrow-inhabiting fishes of the family Gobiidae and other small benthic fishes such as killifishes, flatfishes, and sculpins which escape under a seine or through the mesh of various nets. This study attempted to obtain density values for all littoral fishes, especially for the elusive species listed above. By setting up the procedure for choosing the "best estimate" of density from among four different sampling methods, actual densities of the species have been more closely approximated.

If the biomass density of *Atherinops affinis* for the entire study is calculated by dividing its total biomass by the total area of coverage by all four sampling gears, a biomass density of 3.3 g/m^2 (or about 0.83 g DW/m^2) is obtained. This density value is lower than the estimate of 1.16 g DW/m^2 derived through the best estimate process (Table 6). In this particular case, most densities were mean values of six bag seines which were very effective (99%) at capturing *A. affinis* (Horn and Allen footnote 2). Biomass density for the gobiid,

TABLE 6.—Grand mean estimate of biomass density (g DW/m^2) for common species in the littoral zone (excluding panne) over the 13-mo period (January 1978-January 1979) from the best estimate criteria.

Species	$\bar{X}$ g DW/m^2 ± 1 SE
Atherinops affinis (adult)	0.1043±0.0602
A. affinis	1.1590±0.2573
Fundulus parvipinnis	0.1064±0.0223
Gambusia affinis	0.0015±0.0028
Clevelandia ios	0.0261±0.0117
Anchoa compressa	0.1195±0.0493
Cymatogaster aggregata	0.0167±0.0158
Gillichthys mirabilis	0.0131±0.0035
Anchoa delicatissima	0.0077±0.0053
Mugil cephalus	0.0024±0.0018
Quietula ycauda	0.0029±0.0025
Ilypnus gilberti	0.0021±0.0021
Hypsopsetta guttulata	0.0043±0.0035
Engraulis mordax	0.0019±0.0018
Lepomis macrochirus	0.0006±0.0005
Lepomis cyanellus	0.0003±0.0001
	1.5688 g DW/m^2

Clevelandia ios, determined by total area coverage was 0.013 g/m^2 (about 0.003 g DW/m^2). The value based on best estimate (using square enclosures and small seine estimates) was about 10 times higher at 0.03 g DW/m^2. This large discrepancy is due to the low efficiency of the bag seine for capturing this species. Since the bag seine covered the largest area of any of the sampling gears (220 m^2), its addition to the density determination for *C. ios* led to the large underestimate. The total biomass density of all species by total area was 4.13 g/m^2 (or about 1.02 g DW/m^2) which again was lower than the best estimate grand mean density of 1.57 g DW/m^2.

Average standing stock for the upper bay species during 1978 was 784 kg DW, based on an estimate of 50 ha of habitable littoral zone in upper Newport Bay. This is equivalent to 3,136 kg (wet weight) or 6,899 lb of fish. By the same procedure, the average standing stock of *A. affinis* was 631.6 kg DW and that of *C. ios*, 13.1 kg DW.

The annual production of 9.35 g DW/m^2 for the upper Newport Bay littoral zone in 1978 ranked among the highest values recorded for studies with comparable production determinations of production models (Table 7).

The Newport Bay production estimate in 1978 was surpassed only by the estimate for *Fundulus heteroclitus* (Meredith and Lotrich 1979), an estuarine species of the east coast of the United States. *Fundulus heteroclitus* represented a very efficient energy link between the marsh and the littoral zone in their study. However, as Meredith and Lotrich pointed out, the production value may be an overestimation due to the underestimation of the area of marsh utilized by the fish. The value 4.6 g DW/m^2 obtained by Adams (1976b) for fishes inhabiting east coast eelgrass beds, which are acknowledged as highly productive areas, is half the estimate for the littoral zone of upper Newport Bay.

Short food chains have been implicated as the primary reason for high production in estuarine fish communities (Adams 1976b), a contention which is supported by the findings of this study. Young-of-the-year *Atherinops affinis* accounted for 85% of the annual production and formed a direct link through their herbivorous/detritivorous diet to the high primary productivity of this estuarine system. The remaining, numerically important species of the littoral zone were low-level carnivores. There is little doubt that this assemblage represents an example of "food chain telescoping" as described by Odum (1970).

Even though the fish production in the littoral zone of upper Newport Bay was high compared with most comparable studies, the value presented here is undoubtedly an underestimate. The largest species of the system, adult *Mugil cephalus*, was not represented in the production estimates due to inadequate sampling. Inclusion of this species would have substantially increased the production value. It is unlikely, however, that productivity of adult *M. cephalus* could approach that of juvenile *Atherinops affinis* which were responsible for 85% of the annual fish production.

Influence of Abiotic Factors

The positive correlations between temperature and total abundance, biomass and number of species, and between salinity and total abundance and biomass indicate the general impor-

TABLE 7.—Comparison of annual fish production (P) for marine or estuarine studies with comparable production determinations. Wet weights were converted by multiplying by 0.25. Values are for all species except where noted.

Locale and habitat	Study	Estimated annual P (g DW/m^2)
Delaware salt marsh creek (*Fundulus heteroclitus*)	Meredith and Lotrich (1979)	10.2
Newport Bay littoral zone	present study	9.4
Mexican coastal lagoon	Warburton (1979)	8.6
Cuban freshwater lagoons	Holčík (1970)	6.2
No. Carolina eelgrass beds	Adams (1976b)	4.6
Bermuda Coral Reef	Bardach (1959)	4.3
Texas lagoon (Laguna Madre)	Hellier (1962)	3.8
English Channel pelagic and demersal fishes	Harvey (1951)	1.0
Georges Bank commercial fishes	Clarke (1946)	0.4

tance of these factors to this assemblage. Individual correlations between abiotic factors and species abundances likewise emphasized the importance of temperature and salinity. The correlations between individual species abundances and dissolved oxygen as well as distance into the upper Newport Bay could be due to the intercorrelations of both dissolved oxygen and distance with temperature.

Intercorrelations among factors can confound the interpretation of relationships and introduce redundancy in multivariate analyses. The relationship between dissolved oxygen and distance into the upper Newport Bay is intuitive considering its shallow depths. The positive relationship between temperature and dissolved oxygen was probably due to photosynthesis by green algae during the summer. Winter rainfall in the basically Mediterranean climate of southern California was responsible for the positive correlation between temperature and salinity found in Newport Bay. This relationship is by no means absolute, as evidenced by the low salinities encountered during the tropical rains of September 1978 when temperatures were high.

The results of the second canonical correlation analysis indicate that interaction between temperature and salinity explained most of the variability in species abundance in this system. The correlation between these two abiotic factors probably inflated the R^2 value slightly, but does not negate the overall findings. Ordination of individual species by correlation coefficients with temperature and salinity underscores the influences of these factors on individual species. Furthermore, the substantial decrease in numbers of *A. affinis* at station 1 and the somewhat smaller decrease at station 3 during September rains (low salinity) and relatively high temperatures also illustrate this temperature-salinity interaction.

I propose that an important consequence of temperature-salinity influence found in the present study is the transfer of biomass and, therefore, energy from the littoral zone to the adjacent channel and ultimately to local offshore areas via migration of fishes. This mechanism for energy transfer was best illustrated by the apparent emigration of a large portion of the 0-age class *A. affinis* from the littoral zone from September to December 1978. The transfer also included the biomass produced by essentially all of the periodic species. Weinstein et al. (1980) reached a similar conclusion in their study of the fishes in shallow marsh habitat of a North Carolina estuary. An extensive mark and recapture study should be planned to test this hypothesis in the future.

Seasonal fluctuations of temperate bay-estuarine fish populations may have several causes, but temperature and salinity seem frequently to be the underlying factors. The pattern of increased number of species and individuals with increased temperature in temperate bays and estuaries has been reviewed by Allen and Horn (1975). Recently the large-scale influence of salinity on bay-estuarine fish populations has been demonstrated by Weinstein et al. (1980) for Cape Fear River Estuary, N.C. Unfortunately, any salinity interaction with temperature was not investigated or discussed in the above study.

Studies of subtropical estuaries (Amezcua-Linares 1977; Warburton 1978; Quinn 1980) indicate that salinity may have greater influence on fish populations, since annual temperature ranges are narrower than in temperate bays and estuaries. In each of the above studies on subtropical estuaries, increased abundances corresponded to the season of low rainfall and therefore high salinity. Blaber and Blaber (1981) concluded that turbidity and not temperature and salinity was the single most important factor to the distribution of juvenile fishes in subtropical Moreton Bay, Queensland. However, Blaber and Blaber (1981) did not present statistical evidence to support this contention. The most important environmental factors influencing tropical estuarine (eelgrass) ichthyofaunas are more difficult to identify (Weinstein and Heck 1979; Robertson 1980) and probably include biotic factors such as prey availability, competitors, predators, as well as abiotic factors. Biotic interactions are undoubtedly important in temperate estuarine systems including upper Newport Bay. However, their overall influence on the system is probably swamped by large fluctuations in the physical environment.

Fluctuations in rainfall and temperature regimes during a year and from year to year can have marked effects on the ichthyofauna of estuaries. Moore (1978) has identified long-term (1966-73) fluctuations in summer fish populations in Aransas Bay, Tex. He found that diversity values (H' range of 1.38-2.13) were quite variable from year to year probably as a result of major climatological changes (an unusually wet year; a drought and two hurricanes). These changes in diversity values were probably caused by changes in abundance within a set of resident estuarine species and of periodic species.

In 1978 the ichthyofauna of upper Newport Bay was subjected to rainfall twice that of a "normal" year (70.9 cm for 1978; mean 28.1 cm). The specific effects of this increased precipitation are difficult to assess due to a lack of data from previous years but some guarded comparisons can be made. Population densities of *Atherinops affinis* were lower in 1974-75 than those encountered during 1978 (Allen 1976). Also *Cymatogaster aggregata*, *Clevelandia ios*, and *Leptocottus armatus* occurred in lower numbers in 1978 than in previous years (Horn and Allen 1981). These discrepancies point out the strong year-to-year fluctuations that occur in the fish populations of upper Newport Bay. This conclusion is in complete agreement with the findings of Moore (1978) and sheds doubt on the possibility of completely characterizing a "normal" year in many estuaries because of unpredictable annual variations in climate.

ACKNOWLEDGMENTS

This paper represents a portion of my dissertation research completed at the University of Southern California. For their support and guidance I wish to thank my dissertation committee members: Basil Nafpaktitis, Jon Kastendiek, Robert Lavenberg, Kenneth Chen, and, especially, Michael Horn. A number of people deserve my thanks for participating in the sampling program over the 13-mo period; they are Gary Devian, Frank Edmands, Terry Edwards, Dennis Hagner, John Hunter, Paul Kramsky, Marty Meisler, Margaret Neighbors, Linda Sims, Vic Tanny, Jr., Carol Usui, Brian White, and Craig Wingert. Special thanks go out to Russell Bellmer (U.S. Army Corps of Engineers), Jack Fancher (U.S. Fish and Wildlife Service, USFWS), Peter Haaker (California Department of Fish and Game), Katie Heath, Jeff Jones, Marie Harvey, and Wayne White (USFWS) for their help in carrying out the field work. I thank Ed DeMartini and Michael Horn for offering helpful comments on the manuscript.

Financial support for this research was provided by a contract from the California Department of Fish and Game to California State University, Fullerton (M. H. Horn, Principal Investigator). A 3-mo extension was generously funded by the Orange County Fish and Game Commission.

LITERATURE CITED

ADAMS, S. M.

1976a. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. J. Exp. Mar. Biol. Ecol. 22:269-291.

1976b. The ecology of eelgrass, *Zostera marina* (L.), fish communities. II. Functional analysis. J. Exp. Mar. Biol. Ecol. 22:293-311.

ALLEN, K. R.

1950. The computation of production in fish populations. N.Z. Sci. Rev. 8:1-89.

ALLEN, L. G.

1976. Abundance, diversity, seasonality and community structure of fish populations in Newport Bay, California. M.A. Thesis, California State Univ., Fullerton, 108 p.

1980. Structure and productivity of the littoral fish assemblage of upper Newport Bay, California. Ph.D. Thesis, Univ. Southern California, Los Angeles, 175 p.

ALLEN, L. G., AND M. H. HORN.

1975. Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. Estuarine Coastal Mar. Sci. 3:371-380.

ALLEN, L. G., AND W. S. WHITE.

In press. Ecological aspects of the ichthyoplankton and demersal fish populations of Newport Bay, California: 1974-1975. Los Angeles Cty. Mus. Nat. Hist., Contrib. Sci.

AMEZCUA-LINARES, F.

1977. Generalidades ictiológicas del sistema Lagunar Costero de Huizache-Caimanero, Sinaloa, México. An. Centro Cienc. Mar. Limnol., Univ. Nac. Autón. México 4:1-26.

BANE, G. W.

1968. Fishes of the upper Newport Bay. Museum of Systematic Biology, Univ. Calif. Res. Ser. 3, 114 p.

BANE, G. W., AND M. ROBINSON.

1970. Studies on the shiner perch, *Cymatogaster aggregata* Gibbons, in upper Newport Bay, California. Wasmann J. Biol. 28:259-268.

BARDACH, J. E.

1959. The summer standing crop of fish on a shallow Bermuda reef. Limnol. Oceanogr. 4:77-85.

BECHTEL, T. J., AND B. J. COPELAND.

1970. Fish species diversity indices as indicators of pollution in Galveston Bay, Texas. Contrib. Mar. Sci. 15: 103-132.

BLABER, S. J. M., AND T. G. BLABER.

1981. Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish Biol. 17:143-162.

CHAPMAN, D. W.

1968. Production. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 182-196. Blackwell Sci. Publ., Oxford.

CLARKE, G. L.

1946. Dynamics of production in a marine area. Ecol. Monogr. 16:322-335.

CLIFFORD, H. T., AND W. STEPHENSON.

1975. An introduction to numerical classification. Acad. Press, N.Y., 229 p.

CRONIN, L. E., AND A. J. MANSUETI.

1971. The biology of the estuary. *In* P. A. Douglas and R. H. Stroud (editors), A symposium on the biological significance of estuaries, p. 14-39. Sport Fish. Inst., Wash., D.C.

DAHLBERG, M. D., AND E. P. ODUM.
1970. Annual cycles of species occurrence, abundance and diversity in Georgia estuarine fish populations. Am. Midl. Nat. 83:382-392.

DERICKSON, W. K., AND K. S. PRICE, JR.
1973. The fishes of the shore zone of Rehoboth and Indian River Bays, Delaware. Trans. Am. Fish. Soc. 102:552-562.

FREY, W. W., R. F. HEIN, AND J. L. SPRUILL.
1970. The natural resources of upper Newport Bay and recommendations concerning the Bay's development. Res. Agency Calif. Dep. Fish Game, 148 p.

FRITZ, E. S.
1975. The life history of the California killifish *Fundulus parvipinnis* Girard, in Anaheim Bay, California. Calif. Dep. Fish Game, Fish Bull. 165:91-106.

FRONK, R. H.
1969. Biology of *Atherinops affinis littoralis* Hubbs in Newport Bay. M.S. Thesis, Univ. California, Irvine, 109 p.

HAEDRICH, R. L., AND S. O. HAEDRICH.
1974. A seasonal survey of the fishes in the Mystic River, a polluted estuary in downtown Boston, Massachusetts. Estuarine Coastal Mar. Sci. 2:59-73.

HAEDRICH, R. L., AND C. A. S. HALL.
1976. Fishes and estuaries. Oceanus 19(5):55-63.

HARVEY, H. W.
1951. On the production of living matter in the sea off Plymouth. J. Mar. Biol. Assoc. U.K. 29:97-137.

HELLIER, T. R., JR.
1962. Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. Publ. Inst. Mar. Sci. 8:1-22.

HOLČIK, J.
1970. Standing crop, abundance, production and some ecological aspects of fish populations in some inland waters of Cuba. Vestn. Cesk. Spol. Zool. 34:184-201.

HORN, M. H.
1980. Diel and seasonal variation in the abundance and diversity of shallow-water fish populations in Morro Bay, California. Fish. Bull., U.S. 75:759-770.

HORN, M. H., AND L. G. ALLEN.
1981. Ecology of fishes in upper Newport Bay: seasonal dynamics and community structure. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 45, 102 p.

IVLEV, V. S.
1966. The biological productivity of waters. J. Fish. Res. Board Can. 23:1727-1759.

KJELSON, M. A., AND G. N. JOHNSON.
1978. Catch efficiencies of a 6.1-meter otter trawl for estuarine fish populations. Trans. Am. Fish. Soc. 107: 246-254.

LIVINGSTON, R. J.
1976. Diurnal and seasonal fluctuations of organisms in a north Florida estuary. Estuarine Coastal Mar. Sci. 4:373-400.

MCERLEAN, A. J., S. C. O'CONNOR, J. A. MIHURSKY, AND C. I. GIBSON.
1973. Abundance, diversity and seasonal patterns of estuarine fish populations. Estuarine Coastal Mar. Sci. 1:19-36.

MEREDITH, W. H., AND V. A. LOTRICH.
1979. Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). Estuarine Coastal Mar. Sci. 8:99-118.

MOORE, R. H.
1978. Variations in the diversity of summer estuarine fish populations in Aransas Bay, Texas, 1966-1973. Estuarine Coastal Mar. Sci. 6:495-501.

ODUM, W. E.
1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet, *Mugil cephalus*. *In* J. H. Steele (editor), Marine food chains, p. 222-240. Univ. Calif. Press, Berkeley.

ORTH, R. J., AND K. L. HECK, JR.
1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—Fishes. Estuaries 3:278-288.

OVIATT, C. A., AND S. W. NIXON.
1973. The demersal fish of Narragansett Bay: an analysis of community structure, distribution and abundance. Estuarine Coastal Mar. Sci. 1:361-378.

PEARCY, W. G., AND S. W. RICHARDS.
1962. Distribution and ecology of fishes of the Mystic River estuary, Connecticut. Ecology 43:248-259.

POSEJPAL, M. A.
1969. The population ecology of the benthic ichthyofauna of upper Newport Bay. M.S. Thesis, Univ. California, Irvine, 146 p.

QUAST, J. C.
1968. Observations on the food of the kelp-bed fishes. Calif. Dep. Fish Game, Fish Bull. 139:109-142.

QUINN, N. J.
1980. Analysis of temporal changes in fish assemblages in Serpentine Creek, Queensland. Environ. Biol. Fishes 5(2):117-133.

RECKSIEK, C. W., AND J. D. MCCLEAVE.
1973. Distribution of pelagic fishes in the Sheepscot River—Back River Estuary, Wiscasset, Maine. Trans. Am. Fish. Soc. 102:541-551.

RICKER, W. E.
1946. Production and utilization of fish populations. Ecol. Monogr. 16:374-391.

ROBERTSON, A. I.
1980. The structure and organization of an eelgrass fish fauna. Oecologia (Berl.) 47:76-82.

SHANNON, C. E., AND W. WEAVER.
1949. The mathematical theory of communication. Univ. Illinois Press, Urbana, Ill., 117 p.

SHENKER, J. M., AND J. M. DEAN.
1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. Estuaries 2:154-163.

STEPHENS, J. S., JR., C. TERRY, S. SUBBER, AND M. J. ALLEN.
1974. Abundance, distribution, seasonality, and productivity of the fish populations in Los Angeles Harbor, 1972-73. *In* D. F. Soule and M. Oguri (editors), Marine studies of San Pedro Bay, California, Part IV, Environmental field investigations. Allan Hancock Found. Publ., USC-SG-6-72:1-42.

TARGETT, T. E., AND J. D. MCCLEAVE.
1974. Summer abundance of fishes in a Maine tidal cove with special reference to temperature. Trans. Am. Fish. Soc. 103:325-330.

TYLER, A. V.
1971. Periodic and resident components in communities of Atlantic fishes. J. Fish. Res. Board Can. 28:935-946.

WARBURTON, K.
1978. Community structure, abundance and diversity of fish in a Mexican coastal lagoon system. Estuarine

Coastal Mar. Sci. 7:497-519.
1979. Growth and production of some important species of fish in a Mexican coastal lagoon system. J. Fish Biol. 14:449-464.

WEINSTEIN, M. P., AND K. L. HECK, JR.
1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panamá and in the Gulf of Mexico: composition, structure and community ecology. Mar. Biol. (Berl.) 50:97-107.

WEINSTEIN, M. P., S. L. WEISS, AND M. F. WALTERS.
1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River Estuary, North Carolina, U.S.A. Mar. Biol. (Berl.) 58:227-243.

WILEY, J. L., T. S. Y. KOO, AND L. E. CRONIN.
1972. Finfish productivity in coastal marshes and estuaries. *In* Proceedings of the Coastal Marsh and Estuary Management Symposium, Louisiana State Univ., p. 139-150.

CYCLIC COVARIATION IN THE CALIFORNIA KING SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, SILVER SALMON, *O. KISUTCH*, AND DUNGENESS CRAB, *CANCER MAGISTER*, FISHERIES

LOUIS W. BOTSFORD,[1] RICHARD D. METHOT, JR.,[2] AND JAMES E. WILEN[3]

ABSTRACT

There are apparent cyclic fluctuations in the catch record of both northern and central California salmon fisheries. They are of the same period and strength as well-known cycles in crab catch but of different phase. Statistical characteristics of this covariation, as reflected in estimates of auto- and cross-correlation functions, change following the decline of the central California Dungeness crab fishery. Analysis of a likely cause of this phenomenon, a greater delay in switching of effort from crab to salmon during years of high crab catch, indicates that this mechanism is not present. Phase differences between salmon and crab cycles imply constraints on remaining potential causes, but a cause of the cyclic covariation has not been established.

Regular patterns in fishery catch records reflect underlying mechanisms that can provide the basis for broader understanding, better prediction, and consequently better management of the fishery. Cyclic fluctuations in the northern California Dungeness crab catch have been a topic of research for the past 10 yr. We document here cyclic fluctuations in the northern California salmon catch (Fig. 1) of the same frequency but different phase.

Coastwide fluctuations in Dungeness crab catch were originally attributed to oceanographic causes (Anonymous 1965). Peterson (1973) demonstrated a statistical relationship between coastal upwelling and crab catch. Botsford and Wickham (1975) concluded from estimates of the appropriate cross- and auto-correlation functions that, while crab catch was indeed cyclic and upwelling was correlated with crab catch after a lag of 1 or 2 yr, upwelling itself was not cyclic, hence was not the source of the cycles. Botsford and Wickham (1978) later showed that interage, density-dependent mortality could be the cause of the observed cycles, and derived new stability results that indicated size-selective fishing could decrease population stability, and thereby increase the propensity for cyclic fluctuations. They cited two known potential interage, density-dependent mechanisms, cannibalism and an egg-predator worm, and are conducting field samples of these. On the basis of a disparity between the period of observed cycles and the period of cycles produced by a model that included cannibalism, McKelvey et al. (1980) claimed that cannibalism could not cause the cycles. Botsford (1981) pointed out that the observed disparity was not new, but had been noted by Botsford and Wickham (1978), and critically analyzed the reasoning used by McKelvey et al. (1980) in drawing a new conclusion. In summary, the cause of cycles in the northern California Dungeness crab

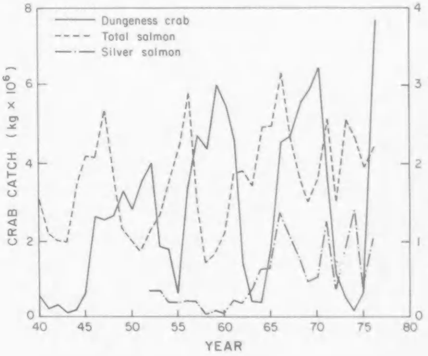


FIGURE 1.—Total landings (kg) in the northern California crab and salmon fisheries for the years 1940-76.

---

[1] Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616.

[2] Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, Calif.; present address: Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[3] Division of Environmental Studies, University of California, Davis, CA 95616.

Manuscript accepted April 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

catch record is still not known and research in this area is continuing.

In contrast to the considerable research attention attracted by cyclic fluctuations in crab catch, fluctuations in the salmon catch record have, to our knowledge, not been previously identified as cyclic. Yet, as seen in Figure 1, these apparently periodic fluctuations in salmon catch have a peak amplitude of about ±0.5 of the mean value. While abundance is predicted each year as part of the management process, these predictions have not taken advantage of this regular pattern that accounts for about two-thirds of the peak catch. An understanding of the underlying cause of cycles in salmon catch has great potential for improved predictive ability and better salmon management.

There are many possible causes of the observed similar cycles in the salmon and crab fisheries. There may be a direct biological interaction between the two species that by itself gives rise to cycles. Alternatively, one may vary cyclically and a direct biological interaction may cause the other to follow it. As another class of possibilities the two processes need not necessarily be directly related but may both be under the influence of a third process (e.g., environmental factors). A third class of possible causes of the observed covariation is some sort of economic linkage between the two fisheries. Since many fishermen fish both species, abundance and effort in one could affect effort in the other.

METHODS AND DATA

Our approach to eliminating unlikely causes of the observed covariation from the many possible causes is based on interpretation of estimated auto- and cross-correlation functions (also called correlograms). This statistical technique has been useful in interpretation of cycles in wildlife populations (Moran 1949; Finerty 1980) and is a recommended initial step in time series analysis (Jenkins and Watts 1968; Box and Jenkins 1970). However, there are few useful results on statistical significance of estimated correlation functions. We use a simple form of a method described by Bartlett (1946). If individual points in a time series are independent and identically distributed, an estimate of the correlation between them is Gaussian with mean zero and variance $1/N$ where N is the total number of samples on which the estimate is based. In the following analysis we show 5% error limits on plots of correlation functions. The occurrence of values of correlation greater in magnitude than this limit more frequently than 1 in 20 indicates a "nonrandom" process. This approach is somewhat limited in that it focuses on single points rather than the pattern of the estimated correlation function as a whole.

If samples in each series are not independent, the significance of both cross- and auto-correlation functions will be overestimated (Granger and Newbold 1974). A suggested solution to this problem in estimating cross-correlations is to prewhiten (i.e., remove correlation between samples) each series by fitting an ARMA model (Box and Jenkins 1970) to the series, then compute cross-correlations between the residuals. We have not taken this approach for two reasons: 1) Computed correlations based on the residuals actually underestimate significance of results (Box and Pierce 1970; Durbin 1970) and 2) prewhitening may actually remove correlations of real interest. With regard to the latter, some auto-correlation within each series exists because of known physical processes (e.g., the fact that catch is the result of fishing several age classes causes intraseries correlation). Removal of this intraseries correlation would reduce the chance of detecting real interseries correlation (e.g., correlation stemming from a causal mechanism that involved catch). Removal of intraseries correlation on the basis of known physical mechanisms will provide more meaningful results; however, it will require further studies of effort dynamics and life histories in both the salmon and crab fisheries. In the meantime, as a simple exploration of the possibility of "spurious" results, we also present correlograms computed from first-differenced data (first-differencing is the process of replacing the data point x_t at time t with the difference $x_t - x_{t-1}$). First-differencing reduces intraseries correlation and has been shown to greatly reduce the incidence of spurious interseries correlation (Granger and Newbold 1974). Correlation results of first-differenced data can be interpreted as the correlation between changes in each series. Also, in all correlations presented, a linear trend has been removed from the series.

Salmon data for these analyses are from monthly catch records collected and published by the California Department of Fish and Game (1954-78). The northern California salmon catch consists of landings at Crescent City, Eureka, and Fort Bragg. The central California catch is from

San Francisco and Monterey. The unit of salmon catch is kilograms of dressed fish with heads on.

Crab catch (kilograms) was summarized by season rather than calendar year so that a season's catch includes catch from November and December of the previous year. The geographic breakdown of crab catch was the same as the salmon catch. Seasonal distribution of crab catch and effort was available only from 1952 to 1976[4] for a northern California region which included an average of 93% of the total northern California catch. In addition to crab catch data, we have also used recent estimates of preseason legal abundance (Methot and Botsford 1982). These estimates were computed from the decline in catch-per-unit-effort within each season according to the Leslie method. Gotshall (1978) also estimated preseason legal abundance for the years 1967-72 using the Leslie method. His results for those years are essentially the same as those used here. McKelvey et al. (1980) also estimated preseason legal abundance, but used a method that depended on the estimated total number of pots in the fishery and annual catch. Since the relationship between these variables can change from year to year in this fishery, we did not use their estimates.

We present first the statistical characteristics of cyclic fluctuations in the northern California salmon and crab catch records as reflected in estimates of their auto- and cross-correlation functions. We then examine characteristics of each of the two salmon species in the fishery. The northern California salmon fishery is composed of king (or chinook) salmon, *Oncorhynchus tshawytscha*, which originate primarily in coastal rivers of northern California and Oregon, and silver (or coho) salmon, *O. kisutch*, which originated primarily in coastal rivers of northern California and Oregon in the 1950's, but depend increasingly on hatchery production in Oregon in the 1960's and 1970's (Pacific Fisheries Management Council 1978).

We then compare the characteristics of the northern California fishery to the central California fishery which differs in two respects: 1) It includes a period of protracted decline in the crab fishery and 2) it involves salmon stocks that originated in the Sacramento and San Joaquin River systems (Pacific Fisheries Management Council 1978). The central California crab fishery declined near 1960 and has remained at a low level since then. Putative causes of this decline and continued low level include an increase in sea temperature (Wild 1980), a predatory worm (Wickham 1979), and an increase in individual growth rate (Botsford 1981). We compare characteristics of the northern California fisheries with the central California fishery both before and after the decline.

We then examine a specific potential cause of the observed covariation. The most obvious and perhaps the most parsimonious explanation of the observed covariation in catch records is switching behavior of fishermen. The proposed hypothesis is simply that, during years of high crab abundance, more fishermen continue to fish for crab rather than beginning to fish for salmon when the salmon season opens. The legal crab season opened in December and continued at least through June in the years of interest. The salmon season opened in April or May, depending on year and species. Although most of the crab catch is landed early in the season, crab and salmon seasons do overlap, thus providing an opportunity to switch. The possibility that this mechanism is responsible for the observed behavior is examined here from three points of view: 1) A comparison of catch during overlapping and nonoverlapping segments of the salmon season, 2) analysis of changes in mean date of the salmon catch, and 3) calculation of the relationship between salmon catch and crab catch per delivery during May and June.

RESULTS

Northern California Total Catch

Estimates of the auto-correlation function for both total northern California Dungeness crab landings and total northern California salmon landings for the years 1940 to 1976 are of the form that would arise from cyclic processes of period 9 or 10 yr (Fig. 2). They both fall to a significant negative value of correlation then rise to a significant positive value of correlation.[5] The auto-correlation of crab abundance is not shown

---

[4] Annual Market Crab-Statewide Reports, California Department of Fish and Game, 1952-77.

[5] Estimates of the same functions for the time period 1952 to 1976 imply that crab is more cyclic (dropping to 0.7 then increasing to 0.8) while salmon is less cyclic (dropping to −0.3 then increasing to 0.4). In this analysis, as in the raw data (Fig. 1), salmon catch appears to be more cyclic in earlier rather than later years, while the crab catch appears to be more cyclic in later years.

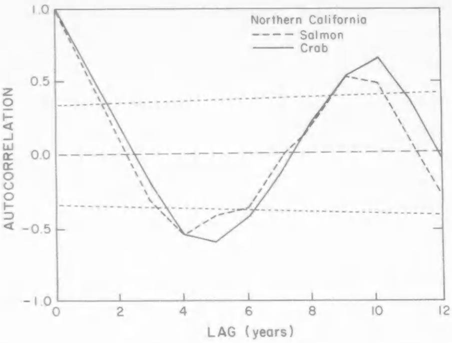


FIGURE 2.—An estimate of the autocorrelation functions for northern California total salmon and crab catch data (Fig. 1). Dotted lines are 0.05 error limits (see text).

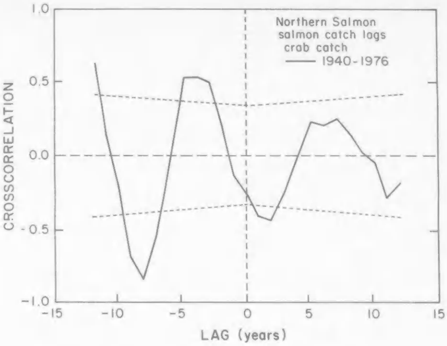


FIGURE 3.—An estimate of the cross-correlation function between northern California total salmon and crab catch data (Fig. 1). A positive lag corresponds to salmon following crab.

but is essentially the same as the auto-correlation of catch (i.e., decreases to significant negative values at 4 and 5 yr, then increases to significant positive values at 10 yr).

The auto-correlation functions computed from first-differenced crab and salmon catch series have the same form but are lower in absolute values. The first negative peak is just barely significant in both, whereas the positive peak of about 10 yr is significant only for the crab catch series.

An estimate of the cross-correlation between total northern California salmon and crab catch is of the form that would arise from two cyclic, covarying processes with a period of 9 or 10 yr and a constant lag of about 4 yr (salmon leading crab) (Fig. 3). Decreasing amplitude of the correlation function with increasing lag is caused by the increasing amplitude of crab catch. The implications of Figure 3 are that crab catch is negatively correlated with salmon catch 1 or 2 yr later and salmon catch is positively correlated with crab catch 3, 4, and 5 yr later.

The same cross-correlation computed for the years for which crab abundance estimates are available (1952-76) is essentially the same as Figure 3. The cross-correlation computed using preseason abundance instead of catch also is quite similar. First-differencing all three cross-correlation functions reduces the amplitude of the function somewhat. The correlation at positive lag is no longer significant and correlation at negative lag is significant only at a lag of −5 yr (except for first-differenced preseason abundance which is not quite significant). The values of cross-correlation for the various versions of these time series are summarized in Table 1.

Northern California Catch by Salmon Species

Because of differences in life history between the two species and the fact that increasing numbers of silver salmon originate in hatcheries, comparison of the relative contributions of each species to the cyclic covariation with crab could provide a clue to the underlying cause. Neither of the estimated auto-correlation functions for king and silver salmon appear as cyclic as the auto-correlation of combined salmon catch (Fig. 4). From this figure king salmon appears somewhat

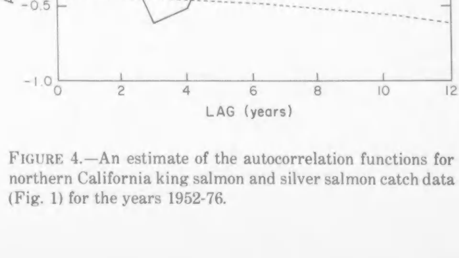


FIGURE 4.—An estimate of the autocorrelation functions for northern California king salmon and silver salmon catch data (Fig. 1) for the years 1952-76.

TABLE 1.—Cross-correlation between salmon catch and crab catch. Positive lags correspond to salmon following crab. Correlations are calculated from detrended original series (O) and from detrended, first-differenced series (F). Tabulated values are multiplied by 100 and are underlined if significant at the 5% level.

Region	Years	Variables			Lag −9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	7	8	9
North	40-76	Crab	Salmon	O	−68	−84	−55	−02	53	53	49	19	−14	−25	−41	−44	−25	00	22	20	24	15	02
				F	−40	−59	−26	00	49	17	28	01	−20	03	−16	−25	−05	08	30	−08	17	−01	−10
North	52-76	Crab	Salmon	O	−72	−90	−62	03	69	60	61	20	−18	−30	−46	−42	−13	19	43	33	29	09	−09
				F	−50	−55	−33	08	57	14	39	−06	−24	06	−24	−28	−05	07	40	−03	19	−04	−17
North	52-76	Crab[1]	Salmon	O	−59	−83	−64	−02	66	45	58	21	−16	−20	−40	−48	−15	16	35	35	20	09	−09
				F	−25	−45	−34	06	50	07	39	−08	−21	17	−16	−38	−01	09	24	09	−01	08	−15
North	52-76	Crab	Salmon[2]	O	−48	−71	−49	−04	42	51	77	19	−35	−32	−52	−39	−01	17	48	40	40	−06	−36
				F	−29	−42	−13	03	19	17	51	−08	−38	14	−23	−23	18	−12	31	−06	35	−14	−31
North	52-76	Crab	Salmon[3]	O	−68	−77	−54	07	67	49	34	15	−03	−20	−29	−32	−18	16	28	19	15	16	11
				F	−48	−44	−37	09	67	05	13	−01	−02	−04	−16	−21	−22	21	32	01	−02	06	01
North	52-76	Crab	King	O	−69	−80	−45	18	62	60	50	−04	−11	−36	−45	−26	03	31	43	22	08	−10	−15
				F	−45	−45	−19	17	49	31	27	−31	08	−12	−35	−14	−01	11	39	−04	05	−15	−05
North	52-76	Crab	Silver	O	−30	−47	−47	−21	34	22	38	42	−17	−02	−17	−38	−29	−10	15	27	41	30	05
				F	−21	−29	−27	−09	26	−17	26	28	−44	22	06	−24	−06	−03	14	−00	22	12	−20
Central	40-61	Crab	Salmon	O			−25	−19	16	64	81	33	−11	−66	−50	−05	09	26	34	27	−00		
				F			−01	−09	18	15	12	16	06	−59	−18	33	18	24	−07	10	−13		
Central	62-76	Crab	Salmon	O					92	−06	−47	−53	−29	24	−01	08	10	38	28				
				F					95	−40	−28	−25	−09	45	−10	08	−12	07	20				

[1] Abundance.
[2] Early season.
[3] Late season.

cyclic while silver salmon is less so. The latter may be due to the shorter time record for silver salmon. First-differencing decreases the value of the peak of negative correlation in king salmon to an insignificant level but the pattern is preserved.

Estimates of cross-correlation between crab catch and catch of each salmon species appear similar to the correlation between crab catch and total salmon catch (Fig. 5). Again, the observed characteristics seem to be stronger in the king salmon rather than the silver salmon records. First-differencing of the crab and salmon series reduces correlation values so that the positive correlation at a negative lag remains significant for king salmon only (Table 1).

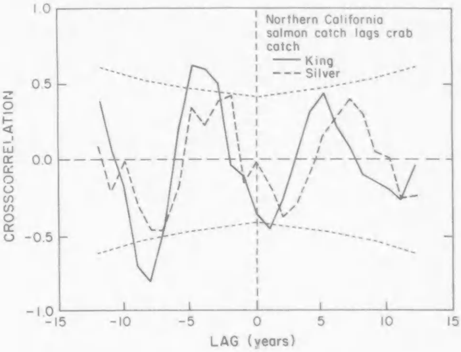


FIGURE 5.—An estimate of the cross-correlation function between northern California crab catch and king salmon and silver salmon for the years 1952-76.

Central California Total Catch

Because of differences between the central California crab fishery (Fig. 6) and the northern California crab fishery, comparison of characteristics of covariation between salmon and crab in northern California with that in central California provides some basis for determining the underlying cause of the covariation in northern California. We can narrow the range of possible causes by determining whether the covariation under discussion here exists both before and after the decline of the crab fishery in 1961. This investigation is, however, somewhat hampered by the extremely short time series that result from bisecting these records.

For the predecline period (1940-61), the auto-

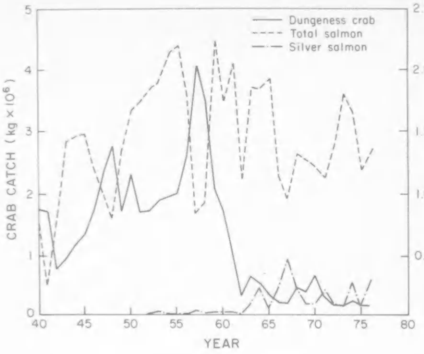


FIGURE 6.—Total landings (kg) in the central California crab and salmon fisheries for the years 1940-76.

correlation functions of salmon and crab catch are virtually the same as in northern California. Salmon and crab fall to −0.37 and −0.59, respectively, (the latter is significant at 0.05) at 4 yr, then increase to +0.43 and +0.54, respectively, (neither significant at 0.05) at 10 yr. First-differencing decreases the strength of both the positive and negative peaks of auto-correlation in both of these series. The estimated cross-correlation between salmon and crab catch in the early period is also similar to that in northern California except for a shift in the negative lag direction near zero lag (Fig. 7). The correlation at zero lag has a significant negative value in central California whereas it is not significant in northern California. This shift would correspond to a negative relationship between crab and salmon, with salmon following crab more closely in central than in northern California. After first-differencing each series the positive correlation peak at negative lag disappears but the negative correlation at zero lag remains (Table 1).

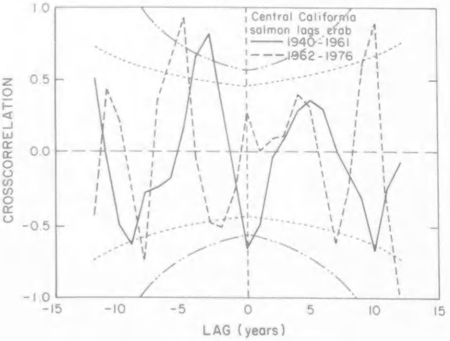


FIGURE 7.—Estimates of cross-correlation functions between central California Dungeness crab and total salmon catch, both before and after the decline in 1961. Outer significance levels apply to the period after the decline.

For the postdecline period (1962-76), the auto-correlation function for crab catch appears cyclic, as it was before the decline, but the period of the cycles has apparently decreased (Fig. 8). The auto-correlation function for salmon decreases to a significant negative value at 3 yr, but shows no clear cyclic tendency for greater lags. First-differencing decreases this first peak by about 0.1 for both series. The cross-correlation estimate for the postdecline period is similar to the northern California relationship for negative lags (i.e., crab following salmon), but is not similar for zero and positive lags (Fig. 7). Both of these latter estimates are for a low number of data points, hence interpretation for large lags is risky (note that the outer significance levels in Figure 7 are for the later period correlation). After first-differencing only the positive correlation at negative lag remains significant (Table 1).

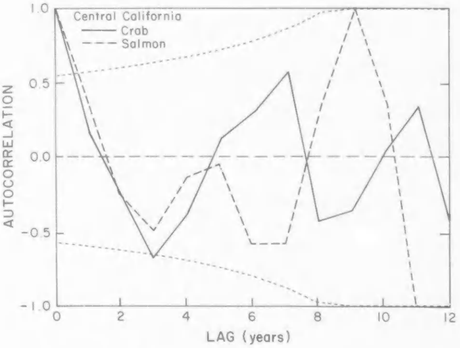


FIGURE 8.—An estimate of autocorrelation functions for central California Dungeness crab and total salmon catch for the years following the decline in crab catch (i.e., 1962-76).

Switching Effort Between Species

If the cyclic nature of salmon catch is caused by fishermen fishing salmon only when crab are not abundant, then cycles in salmon catch should be determined by salmon catch in the part of the season that overlaps the crab season. In other words, salmon catch should appear to be much more cyclic early in the season than late in the season. Salmon catch for the months of April through June and the period from July through September are shown in Figure 9.[6] The only readily apparent feature of this plot is the increasing trend of early season catch.

Estimates of the auto-correlation functions of early and late season salmon catch are shown in Figure 10. Neither of these appears as smoothly cyclic as the total catch. However, since they both decrease to negative values then increase to approximately the same positive value at a 10-yr lag, one does not appear more cyclic than the other.

Estimates of the cross-correlation between total crab catch and early salmon catch and between total crab catch and late salmon catch are shown in Figure 11. There is very little difference between these functions for each time period and they are quite similar to the same function for total annual catch. The only difference between the two species is a slightly more pronounced pattern of correlation for early rather than late season to the right of the origin (i.e., where salmon follows crab). After first-differencing only the positive correlation at a lag of −5 remains (Table 1).

From Figures 10 and 11 we can conclude that the cyclic nature of salmon catch is not contained entirely in the early, overlapping part of the season.

A second, though not independent, means of testing the proposed hypothetical mechanism is to examine the mean data of salmon catch. If crab abundance determined salmon catch early in the salmon season, mean date of the salmon catch would increase with crab catch. The correlation between mean date of salmon catch and total crab catch was not significant ($r = -0.022$ with linear trend subtracted from mean date of salmon catch). Thus this test also yields a negative result.

A third consequence of the proposed mecha-

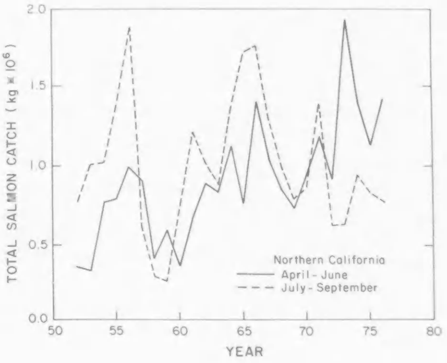


FIGURE 9.—Total salmon catch (kg) in northern California in the early part of the season (April-June) and the late part of the season (July-September) for the years 1952-76.

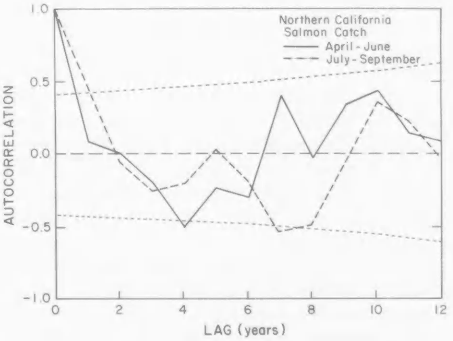


FIGURE 10.—Estimates of the autocorrelation functions for the early (April-June) and late (July-September) parts of the season.

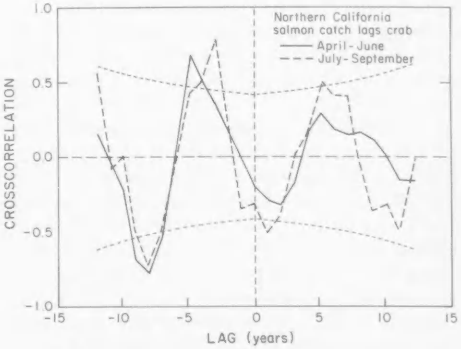


FIGURE 11.—Estimates of the cross-correlation functions between Dungeness crab catch and total salmon catch early in the season (April-June) or total salmon catch late in the season (July-September).

---

[6] The same analysis as that presented here was performed with a bisecting date of 31 May rather than 30 June with no difference in the results.

nism is a relationship between catch per delivery of crab and salmon catch. If fishermen continue to fish crab when crab is abundant, then there would be a relationship between catch per crab delivery and salmon effort in months of overlap between the two fisheries. This relationship would show up in salmon catch provided it was not occluded by fluctuations in salmon abundance. The value (v) per delivery of crab catch was computed for the months of May and June each year as follows:

$$v = \frac{P \cdot W}{CPI \cdot D}$$

where P = market price
W = total weight landed in the months of May and June
CPI = consumer price index
D = number of deliveries in the months of May and June.

For the years 1952 to 1976 there is no significant relationship between salmon catch during May and June and value of each crab delivery (r = 0.31).

DISCUSSION

Interpretation of the correlation functions computed here is somewhat subjective. Since, as described earlier, significance levels do not hold rigorously, they can be interpreted only in a relative sense. Correlations from the first-differenced data can supplement interpretations of the raw (except for detrending) data. First-differencing removes intraseries correlation, hence emphasizes changes between adjacent points in a series. Cross-correlations computed from first-differenced series are more sensitive to the timing of changes, and less sensitive to sustained high and low values. The lag between recurring changes in specific directions in each series must remain constant in order to produce a high cross-correlation. Significant correlations that do not remain high following first-differencing should not necessarily be regarded as spurious, rather they may stem from variables that are highly autocorrelated (e.g., abundance or catch as compared with age-class sizes). On the other hand significant correlations that remain high following first-differencing probably stem from variables with less intraseries correlation.

Computed cross- and auto-correlations support the existence of cyclic covariation between crab and salmon catch in northern California. The fact that the negative correlation at a lag of +2 (Fig. 3) is no longer significant after first-differencing (Table 1) implies that it probably arose from the extended periods of high constant crab catch and low constant salmon catch (Fig. 1).

These same characteristics appear to be present when each salmon species is considered individually. They are, however, weaker in the king salmon and weaker still in silver salmon. The shorter length of the silver salmon time series may be responsible for the latter.

The analysis of central California data is more informative, although it too is constrained by shorter series. Early catch records in central California resemble northern California records in some respects. The auto-correlations of both salmon and crab are the same and the cross-correlation function has the same general shape except that the peak at negative lag is at −3 yr and the peak at positive lag in northern California is at a lag of zero (Figs. 3, 7). This negative correlation at 0 lag is quite apparent in Figure 6. The most striking departure from the northern California situation is the substantial decline of the positive peak at negative lag and the persistence of the negative peak at 0 lag following first-differencing (Table 1). This implies that changes in crab and salmon that are in the same direction are less regular than changes in the opposite direction.

Following the decline in crab catch in central California the auto-correlation functions show weaker cycles of shorter period for the crab and the existence of a cyclic pattern for salmon is questionable. The cross-correlation function is similar to the predecline case but shifted to more negative lags. This could occur, for example, if two cyclic processes retained their shape but were shifted in time with respect to each other. After first-differencing the positive peak at negative lags persists yet the negative peak is diminished in magnitude by half. The postdecline period is similar to northern California in this respect but differs in having a negative correlation at a lag of −2.

The observed differences in lag value of points of significant correlation raise the question of whether the northern California crab or salmon fishery lags its central California counterpart. The cross-correlation between northern California and central California salmon catch for the period 1940 to 1976 has a significant positive peak at +1 and +2 yr that remains significant at +1 yr after first-differencing. The same characteristics are present, though less strong, when the predecline and postdecline periods are considered individually. This lag of 1 or 2 yr between northern California and central California salmon catch is commensurate with the shift in the point of negative correlation for the predecline situation (Fig. 7). The cross-correlation between crab catches at the two locations does not show significant results nor do higher correlations persist after first-differencing.

We can consider the implications of observed correlations for three classes of possible mechanisms. The first class of mechanisms involves cyclic environmental factors which independently drive the cycles in each species. Differences in life history between the two species could be responsible for the phase difference between the two cyclic processes. In the second class of mechanisms, one species is cyclic because of environmental factors or an endogenous mechanism within the population and the second species is cyclic because of some linkage to the first species. The third possibility requires neither species to be inherently cyclic. Rather, a biological interaction between the two species results in cyclic behavior in both (e.g., as in a classical predator-prey system). The computed correlation functions place constraints on specific timing of the mechanisms in each of these classes. These can be compared with known life history characteristics and suspected interactions to eliminate some possibilities.

The life histories of the two species follow similar temporal patterns. The eggs of Dungeness crab and fall-run king salmon hatch in midwinter. The pelagic crab larvae drift for several months then settle as first crabs during April and May. The salmon fry remain in streams for several months then enter the ocean in late spring through summer. Some adult crabs enter the fishery 3 yr after hatching but most are caught at age 4. King salmon first enter the fishery about 2½ yr after hatching, and most are caught at 3½ yr and some are caught 4½ yr after hatching.

That there was no significant positive cross-correlation between the two catch records at 0 lag indicates that a cyclic environmental factor which drives the cycle of one species through an effect on one age-class cannot also affect the same age-class of the other species. This implies, for example, no direct interaction between the 0 age classes of the two species. This is to be expected since most crab larvae have settled before salmon smolts begin entering the nearshore pelagic environment.

The positive cross-correlation, which indicates that good (bad) salmon catches are followed 3 to 5 yr later by good (bad) crab catches, may be a result of a cyclic environmental factor which affects early salmon survival in 1 yr and similarly affects larval crab survival 3 to 5 yr later. This environmental factor need not affect exactly the same age class in both species. For example, a positive effect on growth and survival of maturing salmon in their penultimate year at sea and a simultaneous positive effect on ovary development in female crab could increase salmon catch in the following year and crab catch 4 to 6 yr later through increased egg production in the following year.

Salmon have been observed to prey heavily on pelagic crab megalopae (Orcutt 1978). If this mechanism is considered as increased larval crab mortality when salmon are abundant, it does not fit the conditions implied by the correlations. However, if abundant crab megalopae lead to a good crab year class while increasing the growth and survival of adult salmon, then the observed cross-correlation would result. A mechanism by which salmon were more available to the fishery during years of high crab larval abundance could also cause the observed covariation.

The negative cross-correlation indicates that good (bad) crab catches are followed 1 to 2 yr later by bad (good) salmon catches. That this does not persist following first-differencing is commensurate with it being a result of fluctuation in an auto-correlated series (e.g., abundance) rather than a less auto-correlated series (e.g., recruitment). The mechanism which is a priori the most likely cause of this observation was the one investigated in detail in this paper: the cycle in salmon catch is actually a cycle in fishing effort for salmon and that this cycle is driven by the highly cyclic crab catch.

The conclusion resulting from analyses of the hypothesis of behavioral switching by fishermen is that an immediate response to crab abundance is not a likely cause. The strongest evidence for this was the comparison of the cyclic nature of early with late season salmon catch. The other two analyses are less powerful because both the availability of salmon and the variation in weather conducive to salmon fishing introduce variability in April and May salmon catch. The conclusion drawn from the comparison of early versus late season catch, however, rests on observing the cyclic nature in the late season catch regardless of its cause.

While we have concluded that an immediate behavioral response is not a likely cause, other related possibilities remain. The observed covariation could be caused by an inherently cyclic crab fishery and a negative response of effort in salmon throughout the salmon season (rather than solely in the months of overlap). Further elucidation of the economic question awaits results of an ongoing study of microeconomic behavior of fishermen.

Consideration of the life histories of the species and the timing of events implied by the lags in correlation admits the possibility of direct interaction and dependence of both cycles on environmental factors. Oceanographic conditions have been suggested as causes of fluctuations in other fisheries. Wild (1980) recently proposed that a change in sea surface temperature in the late 1950's reflects a change in the marine environment that is responsible for the decline in the central California Dungeness crab fishery. He also suggested that changes in sea surface temperature were related to fluctuations in the northern California crab catch record. However the actual values of correlation between these processes are not significant. Southward et al. (1975) presented data on cyclic fluctuations in sea temperature and covarying changes in fish population parameters over the past 50 yr in the English Channel.

Though the observed changes in lags and sensitivity to first-differencing may not be related to the causal mechanism, the nature of the covariation between salmon and crab catch does appear to have changed following the decline in central California crab landings. This change is not explained by fishermen switching between species, but could stem from Wild's (1980) proposed change in oceanographic conditions. The decrease in the period of the cycles in crab abundance following the decline is of some interest with regard to the issue of the cause of the decline itself. One of the possible causes of a decrease in period of the cycles is an increase in individual growth rate. This increase in growth rate is a necessary component of one of the potential causes of the decline (Botsford 1981) but is difficult to demonstrate because of the paucity of samples before the decline.

Possible effects of internal population dynamics on the observed behavior are worthy of examination. An interage, density-dependent mechanism has been cited as a potential cause of the cycles in crab abundance (Botsford and Wickham 1978, 1979). A similar mechanism could be operating on salmon abundance if the several stocks in the fishery were in synchrony. Peterman (1978) found positive correlations in smolt-to-adult survivorship between several groups of Pacific salmon populations. Populations that are not density-dependent but reproduce only in their final year have also long been known to fluctuate in a cyclic fashion (Bernardelli 1941; Leslie 1945). However, the period of the cycles is equal to the age of reproduction rather than twice the mean age of reproduction as it is in the stock-dependent recruitment case (Ricker 1954; Botsford and Wickham 1978).

The methods used here could prove useful in other fisheries problems. While time-series techniques have been applied to fishery problems, the primary goal has been a final model of the fishery rather than a search for causal relationships. The latter approach, the one taken here, has the advantage of leading to models that are based on known causal mechanisms rather than correlations of unknown causal mechanisms. Since the nature of these mechanisms could change significantly (possibly because of a change in fishing policy itself), a policy that is cognizant of them will fare better than one that relies on a statistical description from the past.

Another analytical time-series technique that we have not used here is the computation of causality as defined by Granger (1969). His special definition of causality is based on whether addition of data from past time on one variable decreases the error with which another variable can be predicted. The investigations performed here are in the same spirit but do not result in a single quantitative measure of causality.

While we have demonstrated here a potentially important statistical relationship, we have not uncovered the underlying cause. The ultimate cause, however, is worth pursuing. Its discovery and quantitative description could put salmon and crab management on a firmer basis by supplying greater predictive ability. Management could then respond to abundance on a firmer, predictive basis rather than a trial-and-error basis.

ACKNOWLEDGMENTS

The authors would like to acknowledge the contribution of J. Fletcher who pointed out the possible cyclic covariation of the two catch records. We would also like to thank W. A. Gardner and R. Mendelssohn for their reviews and comments.

This work is a result of research sponsored by NOAA Office of Sea Grant, Department of Commerce, under Grant #NOAA-M01-184 R/F52.

LITERATURE CITED

ANONYMOUS.
1965. [Discussion following the report on Dungeness crabs.] Pac. Mar. Fish. Comm., 16th and 17th Annu. Rep., p. 38-39.

BARTLETT, M. S.
1946. On the theoretical specification and sampling properties of autocorrelated time-series. J. R. Stat. Soc. Lond. Suppl. 8(1):27-41.

BERNARDELLI, H.
1941. Population waves. J. Burma Res. Soc. 31:1-18.

BOTSFORD, L. W.
1981. The effects of increased individual growth rates on depressed population size. Am. Nat. 117(1):38-63.

BOTSFORD, L. W., AND D. E. WICKHAM.
1975. Correlation of upwelling index and Dungeness crab catch. Fish. Bull., U.S. 73:901-907.
1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35:833-843.
1979. Population cycles caused by inter-age, density-dependent mortality in young fish and crustaceans. *In* E. Naylor and R. G. Hartnoll (editors), Cyclic phenomena in marine plants and animals, p. 73-82. Proceedings of the 13th European Marine Biology Symposium, Pergamon, N.Y.

BOX, G. E. P., AND G. M. JENKINS.
1970. Time series analysis; forecasting and control. Holden-Day, San Franc., 553 p.

BOX, G. E. P., AND D. A. PIERCE.
1970. Distribution of residual autocorrelations in autoregressive-integrated moving average time series models. J. Am. Stat. Assoc. 65:1509-1526.

CALIFORNIA DEPARTMENT OF FISH AND GAME.
1954-78. California marine fish landings. Calif. Dep. Fish Game.

DURBIN, J.
1970. Testing for serial correlation in least-squares regression when some of the regressors are lagged dependent variables. Econometrica 38:410-421.

FINERTY, J. P.
1980. The population ecology of cycles in small mammals. Yale Univ. Press, New Haven, 234 p.

GOTSHALL, D. W.
1978. Relative abundance studies of Dungeness crabs, *Cancer magister*, in northern California. Calif. Fish Game 64:24-37.

GRANGER, C. W. J.
1969. Investigating causal relations by econometric models and cross-spectral methods. Econometrica 37:424-438.

GRANGER, C. W. J., AND P. NEWBOLD.
1974. Spurious regressions in econometrics. J. Econ. 2:111-120.

JENKINS, G. M., AND D. G. WATTS.
1968. Spectral analysis and its applications. Holden-Day, San Franc., 525 p.

LESLIE, P. H.
1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

MCKELVEY, R., D. HANKIN, K. YANOSKO, AND C. SNYGG.
1980. Stable cycles in multistage recruitment models: An application to the Northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37:2323-2345.

METHOT, R. D., JR., AND L. W. BOTSFORD.
1982. Estimated preseason abundance in the California Dungeness crab (*Cancer magister*) fisheries. Can. J. Fish. Aquat. Sci. 39:1077-1083.

MORAN, P. A. P.
1949. The statistical analysis of the sunspot and lynx cycles. J. Anim. Ecol. 18(1):115-116.

ORCUTT, H. G. (compiler).
1978. Dungeness Crab Research Program. Report for the year 1978. Calif. Dep. Fish Game, Mar. Resour. Admin. Rep. 78-16, 24 p.

PACIFIC FISHERIES MANAGEMENT COUNCIL.
1978. Fishery management plan and environmental impact statement for commercial and recreational salmon fisheries of the coasts of Washington, Oregon and California. Pac. Fish. Manage. Counc., 158 p.

PETERMAN, R. M.
1978. Testing for density-dependent marine survival in Pacific salmonids. J. Fish. Res. Board Can. 35:1434-1450.

PETERSON, W. T.
1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull., U.S. 71:902-910.

RICKER, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.

SOUTHWARD, A. J., E. I. BUTLER, AND L. PENNYCUICK.
1975. Recent cyclic changes in climate and in abundance of marine life. Nature (Lond.) 253:714-717.

WICKHAM, D. E.
1979. *Carcinonemertes errans* and the fouling and mortality of eggs of the Dungeness crab, *Cancer magister*. J. Fish. Res. Board Can. 36:1319-1324.

WILD, P. W.
1980. Effects of seawater temperature on spawning, egg development, hatching success, and population fluctuations of the Dungeness crab, *Cancer magister*. Calif. Coop. Oceanic Fish. Invest. Rep. 21:115-120.

SWIMMING KINEMATICS OF SHARKS[1]

P. W. WEBB[2] AND RAYMOND S. KEYES[3]

ABSTRACT

Video-tape recordings were made of locomotor movements of six species of free-swimming sharks. The following kinematic parameters were measured, normalized where appropriate with total body length (L): tail-beat frequency (f), specific tail-beat amplitude (A/L), specific wavelength of the propulsive wave (λ/L), specific stride length (S/L), and the rate of change of A/L with position along the body. These parameters were measured over a range of swimming speeds up to 3.9 m/s (4 L/s) for one species, the blacktip shark, *Carcharhinus melanopterus*. Data were obtained only over a narrow range of low swimming speeds for the other species, because they could not be induced to swim at high speeds. For the blacktip shark, f increased with speed, but A/L, λ/L, and, hence, S/L all decreased as speed increased. Among the six species, λ/L and S/L tended to be larger for more fusiform species, while A/L and f, at a given speed, appeared to be lower. This implies swimming movements of more fusiform species generated more thrust per beat than elongate species and/or the swimming drag was lower. The pattern of amplitude changes along the body length of sharks was intermediate between that observed for elongate and fusiform teleosts.

Thrust and swimming efficiency can be improved when discrete fins interact, as between the dorsal and caudal fins of sharks. For this to occur, a phase difference of $\geq 0.5\pi$ must occur between the vortex wake shed at the trailing edge of an anterior fin and the leading edge motion of a more posterior fin, which interacts with the upstream vortex sheet. The variations in swimming kinematics with speed, the differences among the species studied, and the conservative nature of body form in sharks probably function to increase thrust and efficiency by such interaction between median fins.

Most studies on fish locomotion have concentrated on bony fish, especially teleosts. As a result, modern ideas on fish locomotor functional-morphology are dominated by knowledge of only one of the major groups of fish. However, there are many unique features among cartilaginous fish that suggest they have exploited some different biomechanical possibilities. Sharks appear to swim like elongate teleosts, but in contrast they have discrete, often widely spaced median fins more typical of fusiform teleosts. Lighthill (1970) and Sparenberg and Wiersma (1975) have shown that this combination provides an opportunity for median fins to interact in such a way that thrust and Froude efficiency (the ratio of useful work to total work of the propellor system) are improved.

If shark locomotion were to utilize flow interactions between median fins to hydromechanical advantage, they would have to swim somewhat differently from teleosts. For example, teleosts modulate tail-beat frequency with speed, but sharks might also have to vary other kinematic parameters, such as the length of the propulsive wave and tail-beat amplitude. Therefore, the following experiments were performed to determine how swimming kinematics and phase differences between fin motions varied with speed for six species of sharks. While difficulties were encountered in obtaining data over a wide range of speeds, the results suggest that sharks vary swimming kinematics to utilize interactions between median fins, as postulated by Lighthill (1970).

METHODS

Observations were made on six species of free-swimming sharks (Fig. 1). Three species, the bull shark, *Carcharhinus leucas*; lemon shark, *Negaprion brevirostris*; and nurse shark, *Ginglymostoma cirratum*, were approximately 2-2.5 m in total length. They were contained in the public display at Sea World, San Diego, Calif., described by Weihs et al. (1981). Specimens of the other three species were smaller; Pacific blacktip shark, *Carcharhinus melanopterus* (total length, $L = 0.97 \pm 0.5$ m; $\overline{X} \pm 2$SE; $N = 7$); bonnethead,

---

[1] Contribution No. 8104-SD from Sea World, San Diego, Calif.

[2] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, Calif.; present address: School of Natural Resources, University of Michigan, Ann Arbor, MI 48109.

[3] Sea World, San Diego, CA 92109.

Manuscript accepted February 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

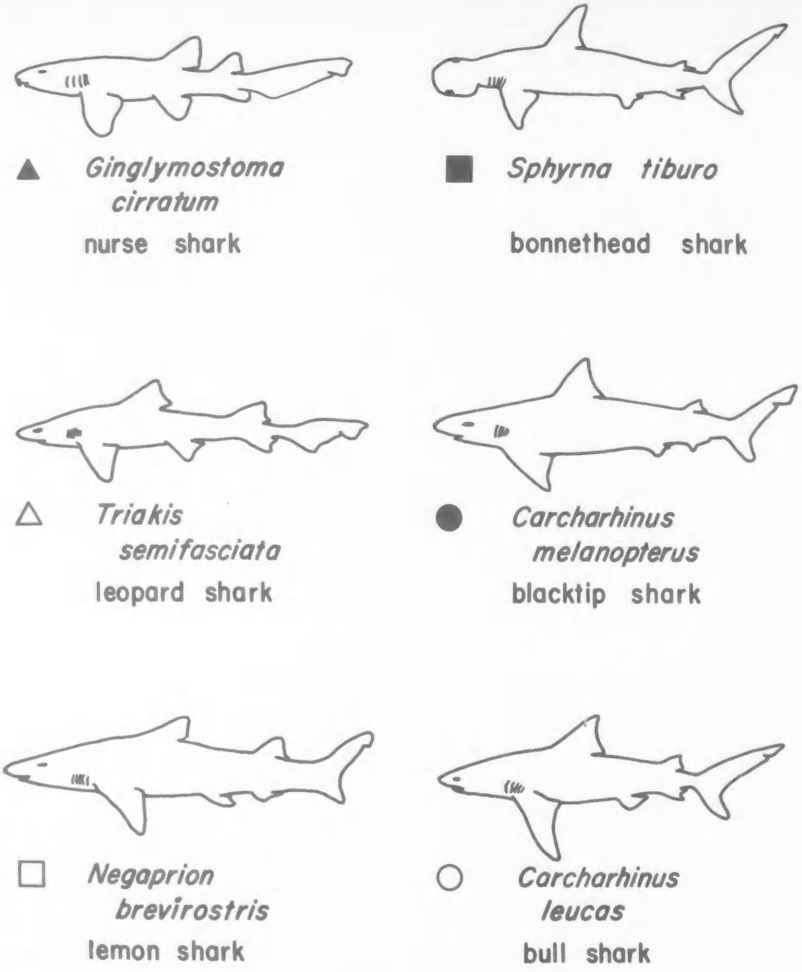

▲ *Ginglymostoma cirratum*
nurse shark
■ *Sphyrna tiburo*
bonnethead shark
△ *Triakis semifasciata*
leopard shark
● *Carcharhinus melanopterus*
blacktip shark
□ *Negaprion brevirostris*
lemon shark
○ *Carcharhinus leucas*
bull shark

FIGURE 1.—Drawings (not to scale) showing the longitudinal body form of the six species of sharks for which swimming kinematic data were obtained. The symbols are used through most of the following figures.

Sphyrna tiburo ($L = 0.93 \pm 0.09$ m; $N = 5$); and leopard shark, *Triakis semifasciata* ($L = 0.98 \pm 0.11$ m; $N = 5$). The three smaller species were part of a second public display in an outside pool at Sea World. This pool was approximately oval in shape, 9 m long, 5.5 m wide, and 0.3 m deep. Small individual sharks were also observed in a small rectangular tank, 2.5 m long, 1.2 m wide, and 0.3 m deep. This tank had a transparent bottom. The water temperature in all three facilities was the same and constant at 24.5°C. Thomson and Simanek (1977) have shown that most sharks fall into one of four functional-morphology groups. Group 1 includes sharks with streamlined, fusiform, deep bodies; a narrow caudal peduncle with lateral flukes (streamlining); and a high aspect ratio tail. This group is represented by large pelagic species, such as *Lamna* which were unavailable for study. Group 2 is similar to group 1, but lacking the deep body and streamlined caudal peduncle. *Carcharhinus leucas*, *C. melanopterus*, and *S. tiburo* represent group 2. Group 3 includes sharks with a low aspect ratio tail, making a small angle to the horizontal, and a less fusiform body, represented by *G. cirratum*, *T. semifasciata*, and *N. brevirostris*. Group 4 incorporates the squaloid sharks, e.g., *Centrolepis*, which were not available.

Swimming movements were recorded on video tape. Recordings were made above the free surface of the public display facilities. Surface ripples were small compared with the images of the sharks and were therefore ignored. To avoid surface problems, observations in the rectangular tank were made from below through the transparent bottom. Surface ripples did not deleteriously affect measurement accuracy because no differences in data from the public facilities and the rectangular tank could be found.

Swimming records were obtained for as wide a range of speeds as possible. In most cases, normal variation in motor behavior due to the operation of the park was exploited. For the large sharks, observations were made before the display opened, during normal hours, and during feeding. Because of the possibility of injury leading to mortality, other invasive methods to induce higher speeds were not used. Similar procedures were employed for the smaller sharks. Underwater concussions, induced by dropping heavy objects (fluid-filled metal kegs), and visual stimuli were used to induce higher speeds in these sharks. Tactile stimuli were also employed to generate a range of speeds in the rectangular tank.

Video tape was analyzed "frame-by-frame," using manual advance to resolve movements to within 1/60 s (17 ms). Because a large length range was used, kinematic observations were normalized, for convenience, with respect to total length, L, measured from the tip of the nose to the tip of the tail. Specific swimming speed (speed/L), specific amplitude (amplitude/L), and tail-beat frequency (f) were measured for periods of steady swimming of two or more tail beats. The speed of the propulsive wave (c) was calculated from the backward displacement of wave crests, and specific wave-length (λ/L) was calculated from c/Lf.

RESULTS

Representative swimming movements for three of the species of sharks are illustrated in Figure 2. The body was bent into a wave that travelled backwards over the body at a speed greater than the swimming speed. The amplitude increased caudally to reach maximum values at the trailing edge (the tip of the caudal fin). In general, the form of propulsive movements was similar to that of other fish, as originally described by Gray (1933).

Kinematic parameters varied among the six species and with swimming speed. In practice, it proved extremely difficult to induce the sharks to swim over a wide speed range. This is consistent with experiences of Johnson (1970) with the brown shark, *Carcharhinus plumbeus* (= *C. milberti*), and Brett and Blackburn (1978) with the spiny dogfish, *Squalus acanthias*. Hunter and Zweifel (1971) reported kinematic data for a single leopard shark, *Triakis henlei*, swimming in a water tunnel, but the speed range is not given. Only the blacktip sharks swam over a speed range large enough to permit examination of the relationships between kinematics and speed. Data for the other species was therefore simply averaged (Table 1). The sharks also did not swim at very low speeds.

Tail-beat frequency increased linearly with speed (Fig. 3A), as found for other species of sharks and for teleosts (see Johnson 1970; Hunter and Zweifel 1971; Webb 1975; Aleyev 1977). However, frequencies increased at a higher rate with speed than observed for other fish. Mean specific speeds and tail-beat frequencies varied among the six species of sharks. Compared with the slope of the blacktip shark relationship, more elongate species (e.g., nurse shark; group 3 of Thomson and Simanek 1977) tended to have higher tail-beat frequencies at a given specific speed than more fusiform fish (e.g., bull shark; group 2 of Thomson and Simanek 1977) (Fig. 3B; Table 1).

Specific amplitude of the blacktip shark decreased with increasing speed (Fig. 3C) and hence was inversely related to tail-beat frequency. Specific amplitudes varied from 0.06 to 0.21 among species, with the more fusiform sharks having lower values (Fig. 3D). With the exception of the bull shark, mean specific swimming speeds were greater for the more fusiform species. Thus, for the interspecific data, specific amplitude decreased with specific speed, similar to the intraspecific observations on blacktip sharks. Among teleosts, both tail-beat amplitude and frequency may increase together at very low speeds (Bainbridge 1958; Webb 1971, 1973). However, over most of the speed range, caudal

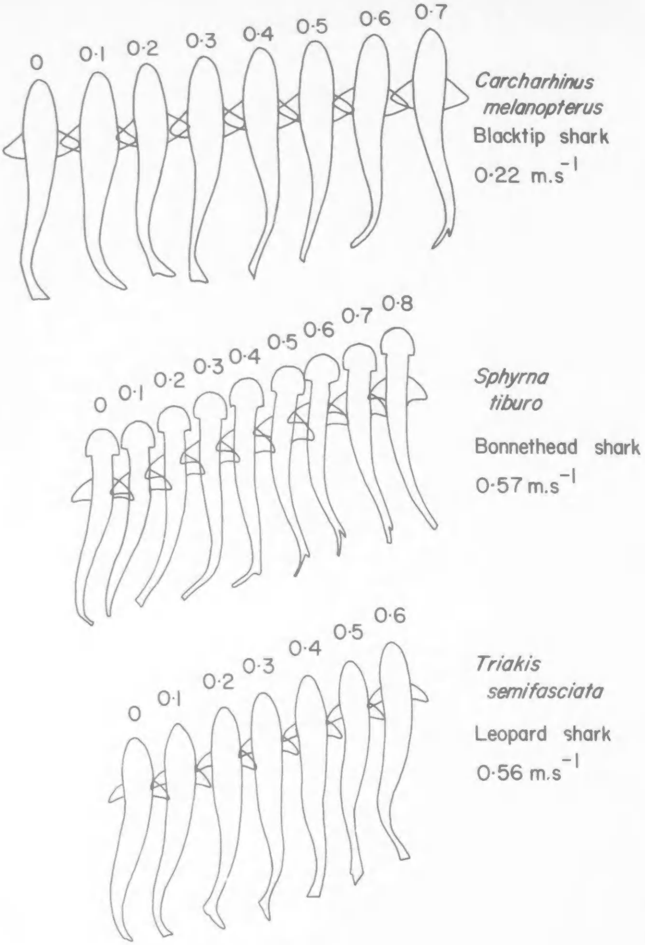

0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
Carcharhinus melanopterus
Blacktip shark
0·22 m.s⁻¹
0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
Sphyrna tiburo
Bonnethead shark
0·57 m.s⁻¹
0
0·1
0·2
0·3
0·4
0·5
0·6
Triakis semifasciata
Leopard shark
0·56 m.s⁻¹

FIGURE 2.—Tracings from videotapes of three species of sharks swimming at three different speeds to show typical body movements. The times above each tracing are in seconds.

fin trailing edge amplitudes tend to be constant at about 0.2 *L* (see Hunter and Zweifel 1971).

In those cases where specific amplitudes and tail-beat frequencies have been related, their product (fA/L) is linearly related to speed. A similar relationship was calculated for this product using the relationships derived for *Triakis* by Hunter and Zweifel (1971) and was similar, but slightly curved for the blacktip shark (Fig. 3E). The product fA/L also increased with speed for the other species (Fig. 3F). The free-swimming sharks thus showed frequency and amplitude modulation with speed. This contrasts with *Triakis henlei* in a water tunnel where only tail-beat frequency was modulated, perhaps due to the presence of walls in the water tunnel. The modulation of both tail-beat frequency and amplitude with swimming speed explains the differences in the kinematics-swimming speed relationships between teleosts and sharks. It appears that the shark propulsive system is more plastic than that of bony fish.

Because of the interrelationships between tail-beat frequency, specific amplitude, and specific swimming speed, stride length also varied inversely with swimming speed for the blacktip

TABLE 1.—Summary of mean kinematic parameters for six species of sharks. Data show mean values ±2SE. Sharks are ranked according to their morphology from the most elongate to most fusiform species. This morphology would be expected to be associated with more anguilliform and more carangiform swimming, respectively.

Species	Specific swimming speed (*U/L*)	Tail-beat frequency (*f*; Hz)	Specific tail-beat amplitude (*A/L*)	$\frac{fA}{L}$	Specific stride length (*S/L*)	Specific wave-length (λ/L)	Phase difference (radians)	*N*
Nurse shark	0.34 ±0.04	0.67 ±0.14	0.21 ±0.04	0.15 ±0.04	0.51 ±0.08	—	—	12
Leopard shark	0.58 ±0.15	1.12 ±0.30	0.20 ±0.04	0.22 ±0.08	0.55 ±0.10	0.77 ±0.14	0.53 ±0.18	10
Lemon shark	0.47 ±0.14	0.95 ±0.26	0.18 ±0.06	0.16 ±0.04	0.58 ±0.09	—	—	6
Bonnethead shark	0.84 ±0.11	1.25 ±0.14	0.18 ±0.02	0.23 ±0.04	0.64 ±0.03	0.91 ±0.06	0.46 ±0.08	14
Blacktip shark	0.80 ±0.10	1.13 ±0.14	0.18 ±0.02	0.33 ±0.12	0.72 ±0.03	1.07 ±0.09	0.47 ±0.05	18
Bull shark	0.58 ±0.09	0.78 ±0.21	0.16 ±0.03	0.13 ±0.05	0.74 ±0.14	—	—	5

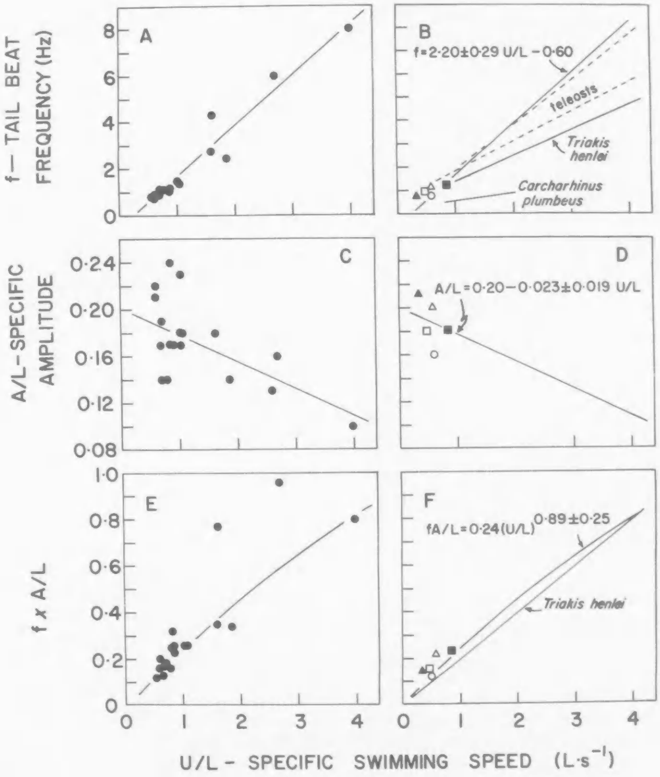


FIGURE 3.—Relationships between tail-beat frequency, f, specific amplitude, A/L, and their product, fA/L, as functions of specific swimming speed, U/L for various sharks. A, C, and E show data for blacktip sharks and best-fit functional regressions. These curves, and the pertinent equation, are shown with the mean values for the other species in B, D, and F. Values for the slope of the equations are the mean ±2SE. The key to symbols is in Figure 1. Other data are teleosts and *Triakis henlei* from Hunter and Zweifel (1971) and *Carcharhinus plumbeus* from Johnson (1970).

shark and among the six species (Fig. 4). Stride length is defined as the distance travelled per tail beat (Wardle 1975). In teleosts, specific stride length (stride length/*L*) typically takes values of 0.6 to 0.8, and does not vary with speed (Wardle 1975). In blacktip sharks, specific stride lengths comparable with those of teleosts were seen only at low speeds and stride length was lower at higher speeds. Specific stride length was similar to the teleost values in the more fusiform sharks, but was lower in more elongate species, the lowest value of 0.51 *L* being found for nurse sharks (Table 1, Fig. 4).

Data on specific wavelengths were only measured with sufficient accuracy for the three smaller species. Values ranged from 0.77 to 1.07 *L*, and tended to be larger for the more fusiform species. Specific wavelength decreased with specific swimming speed in blacktip sharks (Fig. 5), contrasting with teleosts, where specific wavelength is usually independent of speed (Webb 1971, 1973; Wardle and Videler 1980).

Rates of change in amplitude were measured along the body length. In the sharks, there was an area along the body, about 0.2 *L* from the nose, where both amplitude and its rate of change with body length were least (Fig. 6). Anterior to this area, rates of change in amplitude were negative where amplitude increased rostrally due to yawing of the nose. These patterns are similar to those of teleosts. The maximum rate of increase in amplitude in sharks occurred from 0.5 to 0.7 *L*, and declined over more posterior portions of the body. This particular pattern has not been described in teleosts, which usually show an early rise in amplitude (e.g., eel) or sustain increasing rates of amplitude over the whole caudal region (e.g., fusiform teleosts). The area over which amplitude begins to increase in sharks is close to the region of the trailing edge of the first dorsal fin (Thomson and Simanek 1977).

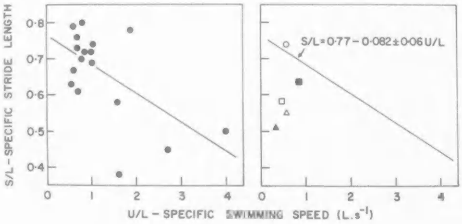


FIGURE 4.—The relationship between specific stride length, S/L, and specific swimming speed, U/L for several sharks. The key to symbols is in Figure 1.

DISCUSSION

The diversity of swimming kinematics in fish was originally described and classified by Breder

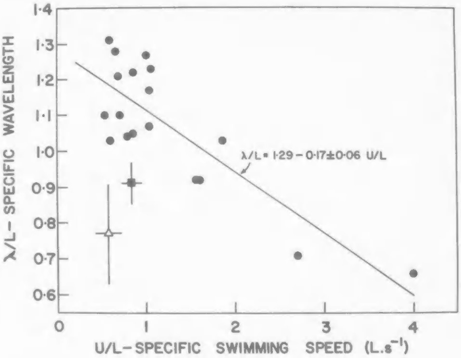


FIGURE 5.—The relationship between specific wavelength, λ/L and specific swimming speed, U/L for three species of shark. Vertical and horizontal bars are ±2SE. The functional regression was fitted only to data for the blacktip shark. The key to symbols is in Figure 1.

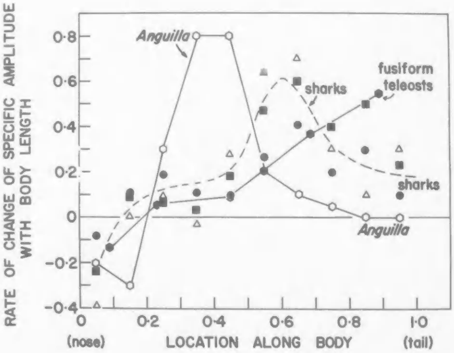


FIGURE 6.—The relationship between the rate of change of amplitude along the body length and the position along the body in some fishes. The data for fusiform teleosts (solid hexagons linked by solid lines) were taken from Bainbridge (1963) for dace, *Leuciscus leuciscus*, and bream, *Ambramis brama*. Data for Anguilla (open hexagons linked by a solid line) were taken from Gray (1933). Data for the sharks (see key in Fig. 1) were taken from Figure 2; the dotted line was fitted by eye through the data for sharks.

(1926), and has been more recently updated by Lindsey (1978). The definition of common locomotor patterns, or modes (Lighthill 1975), for undulatory swimming movements of the body and caudal fin are based on the number of one-half wavelengths contained within the body length and the pattern of increasing amplitude along the body. The elongate eel, *Anguilla*, is definitive for the anguilliform mode where the body contains more than one-half wavelength within the body length, and often one or more complete waves. The lateral amplitude of body movements rises early and is large over most of the body length. Jacks, in the family Carangidae, are representative of the carangiform mode where the body length contains less than one-half wavelength, and lateral displacements increase rapidly over the posterior third or half of the body. Breder (1927) used the term "sub-carangiform mode" for fish with wave patterns of the anguilliform mode and amplitude changes similar to the carangiform mode. So far, detailed studies of fusiform teleosts have been on subcarangiform swimmers.

The six species of shark are also subcarangiform swimmers according to these definitions; the body contained more than one-half of a wave (Table 1, Fig. 5) and the amplitude of body movements increased predominantly over the posterior half of the body (Fig. 6). However, the maximum rate of increase in amplitude occurred over the third quarter of the body, intermediate between the situation for elongate and fusiform teleosts. Therefore, although the sharks swam in the subcarangiform mode, they were more eel-like than fusiform teleosts. This is consistent with the unaided visual impressions of shark swimming.

Among teleosts, trends in swimming kinematics from the anguilliform mode towards carangiform modes are associated with changes in body form from an elongate, flexible body to a more fusiform, less flexible body. This is coupled with a larger caudal fin depth increasingly separated from the body by a narrow caudal peduncle, a morphology defined as narrow necking (Lighthill 1975). The same trends are seen in the six species of sharks studied here (Fig. 1, Table 1). The more fusiform species were those with longer propulsive wavelengths and a larger tail depth swimming in a more carangiform mode than the elongate sharks. In terms of the classification of shark functional morphology by Thomson and Simanek (1977), group 1 is most carangiform and groups 3 and 4 are most anguilliform. Group 1 representatives were not studied here.

The two factors of increasing wavelength and caudal fin depth in the carangiform swimmers are known to increase thrust and Froudé efficiency (Lighthill 1975). However, thrust is reduced by a decrease in tail-beat amplitude. Among the sharks, increasing wavelength and tail depth were found with smaller amplitudes. Thus, the more fusiform, more carangiform species show features that would both enhance and decrease performance. Stride length increased in these more fusiform sharks so that overall the larger wavelength and deeper caudal fins must generate more than enough thrust, perhaps more efficiently, to offset reduced amplitudes.

The details of kinematic movements appear very different for sharks compared with bony fish. In the teleosts that have been studied to date (see Hunter and Zweifel 1971; Aleyev 1977) tail-beat frequency is the major kinematic variable with speed, and over most of the range of swimming speeds, it is the only variable. In contrast, the blacktip shark modulated all three of the kinematic variables that influence thrust: tail-beat frequency, tail-beat amplitude, and the length of the propulsive wave. Teleosts vary one morphological parameter with speed that would also affect thrust. This is the depth of the caudal fin trailing edge (Bainbridge 1963; Webb 1971) to vary the mass of water accelerated by propulsive movements (see Alexander 1968; Lighthill 1975). The skeleton of shark fins is based on cartilaginous ceratotrichia, rather than bony rays, which cannot be individually controlled. As a result, shark fins lack the flexibility to substantially modify fin depth during swimming.

The differences in locomotor kinematics with speed of the sharks illustrated by the blacktip shark, compared with teleosts, may be related to hydrodynamic interactions between the median dorsal fins and the caudal fin. This interaction was first described by Lighthill (1970) and has been developed in detail using hydromechanical theory for inviscid fluids by Sparenberg and Wiersma (1975). A vortex sheet is shed by the trailing edge of any sharp fin or body edge. This vortex sheet travels downstream, but it also has a lateral velocity component determined by the motion of the trailing edge; i.e., the wake follows a sinusoidal path (see illustrations in Rosen 1959; Aleyev 1977). The vortex sheet carries momentum determined by the motions and dimensions of the body and fin at the fin trailing edge.

The momentum carried in the vortex sheet will contribute to instantaneous thrust, and if there is no downstream fin to influence the flow, this momentum will contribute to the mean thrust and power of the fish (Wu 1971; Newman and Wu 1973). However, when there is a downstream re-entrant fin (i.e., a second downstream median fin spanning the flow from the anterior fin) the vortex sheet will impinge on the leading edge of that fin. If the gap between the fins is small, there is little difference between the motion of the incident vortex sheet and the motion of the leading edge of the downstream fin. Then the mean strength of the vortex sheet shed by the downstream fin is determined by the motion of that fin, with no significant contribution from the upstream vortex sheet from the anterior fin, i.e., the upstream fin has no effect on the wake eventually shed by the fish. In this case, the interaction between median fins does not influence mean thrust.

Lighthill (1970) showed that a different situation can occur when the gap between median fins is large. Under these circumstances, there may be a large enough phase difference between the motion of the incident vortex sheet and the downstream fin, so that the momentum shed upstream is not annihilated by the second fin. Then, the work done by the anterior fin against the momentum shed by its trailing edge together with that due to an increased incident velocity at the downstream fin increase total power output and improve efficiency (Lighthill 1975:80-84; Sparenberg and Wiersma 1975).

The phase difference in the motion of the trailing edge of one fin located at a position a_1, along the body, and the leading edge of a second more posterior fin at position a_2, is $2\pi(a_2 - a_1)/\lambda$ where λ is the length of the propulsive wave. However, the vortex sheet travels downstream at the mean speed, U, of the fish, while the body undulation travels backwards at a speed c, greater than U. Therefore, the phase difference, ϕ, in the motions of the vortex sheet shed by the anterior fin and the leading edge of a posterior fin is given by (Lighthill 1975, equation 28):

$$\phi = 2\pi\left(\frac{a_2 - a_1}{\lambda}\right)\left(\frac{c}{U} - 1\right). \qquad (1)$$

Sharks typically have three median fins, the first and second dorsal fins and the caudal fin. Thomson and Simanek (1977) have analyzed several morphological features of 56 species of sharks and show that the second dorsal fin is characteristically small compared with the first dorsal fin, especially in pelagic species. In addition, the second dorsal fin would only be partly re-entrant to most of the vortex sheet shed by the upstream fin because of the posterior taper of the body. Therefore, it seems likely that the second dorsal fin has relatively little effect on the flow between the other two fins during steady cruising. Thomson and Simanek's observations also indicate that the caudal fin depth is typically greater than or equal to that of the trailing edge of the first dorsal fin, as required to maximize the interaction. Therefore, ϕ was calculated for interactions between the first dorsal fin and the caudal fin of the blacktip, bonnethead, and leopard sharks (Table 2; Fig. 7). ϕ was close to, or $>0.5\pi$, as required for the interaction hypothesized by Lighthill (1970). A single record for the dogfish, *Acanthias vulgaris*, in Gray (1933) also gives a value of $\phi = 0.52\pi$ (Webb 1975). For

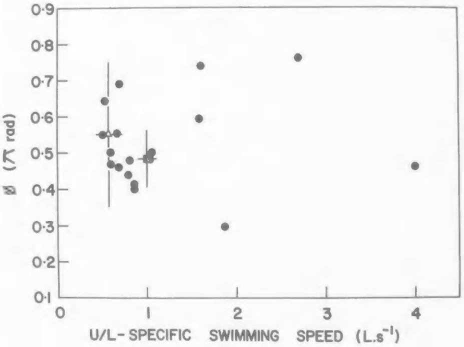


FIGURE 7.—The relationship between the phase difference ϕ (see Equation (1)) and specific swimming speed for three species of sharks. Vertical and horizontal bars are ±2SE. The key to symbols is in Figure 1.

TABLE 2.—Separation, $(a_2 - a_1)/L$, between the trailing edge of the first dorsal fin (a_1) and the mean position of the leading edge of the caudal fin (a_2), and phase difference (ϕ) between their movements for three species of sharks. ϕ was calculated from data in this table and in Figures 3 and 4 using Equation (1).

Species	$(a_2 - a_1)/L$	ϕ ($\bar{X}$±2SE) (π radians)
Leopard shark	0.48	0.55±0.20
Bonnethead shark	0.50	0.48±0.08
Blacktip shark	0.47	0.51±0.05

blacktip shark, ϕ was of the order of 0.5π over the range of swimming speeds studied.

In Equation (1), a_1 and a_2 are constants, and therefore, f or λ can be varied at any speed to keep $\phi \geq 0.5\pi$. However, such changes also affect thrust. For example, if λ varies with speed, compensatory changes in tail-beat frequency and/or tail-beat amplitude must occur to balance thrust and drag at a given speed. The blacktip shark modulated both. Therefore, the modulation of wavelength, amplitude, and frequency with speed can be explained in terms of mechanical advantages from an interaction between widely spaced median fins. It should also be noted that the early rate of increase of amplitude along the body in sharks, occurring near the first dorsal fin, might increase the strength of the vortex sheet. This could enhance thrust, perhaps more than would occur with patterns of increasing amplitude seen in fusiform teleosts.

Adaptive flow interactions between median fins as suggested by Lighthill (1970) apply to the established flow patterns of a steadily swimming fish. Therefore, the common body form and kinematic patterns of sharks appear to be adaptations for cruising. Some sharks, analogous in form to tuna (group 1 of Thomson and Simanek 1977), are obviously highly specialized for cruising (Lighthill 1975; Lindsey 1978), but the present observations suggest that other sharks are also specialized through the utilization of other principles, exploiting more anguilliform propulsion and a more elongate, flexible body. The distribution of the median fins along the body is very similar among sharks (Thomson and Simanek 1977). This suggests that such cruising adaptations are relatively common. Furthermore, sharks are frequently negatively buoyant, when continuous forward motion is important in swimming free from the bottom. This argues for the importance of cruising in the routine behavior of sharks, and hence the importance of any mechanisms to enhance thrust and efficiency in steady swimming.

Comparative observations on teleosts also suggest that in general, sharks are specialized in cruising. Experimental studies have shown that optimal design for transient swimming patterns (angular and linear acceleration) differs from, and is largely exclusive of, that for steady swimming such as cruising (see review by Webb in press). In teleosts, optimal morphological features for steady swimming include a small area anterior to a deep high aspect ratio tail propelling a fairly rigid body. For maximum acceleration, depth (and hence area) should be large over the whole length of a flexible body. Bony fish can achieve some compromise because of their flexible fins, but in general design for unsteady acceleration activity appears most important (Webb 1982). Compromises are excluded for sharks because they do not have collapsible fins. In addition, the separation of the median fins reduces the area of the body available to generate large forces for acceleration. Some sharks, e.g., the horn shark, *Heterodontus francisci*, have somewhat enlarged median fins that suggest a greater importance of acceleration. In general, a more posterior location of the first dorsal fin is associated with larger area fins, as in *Ginglymostoma cirratum* that could similarly improve acceleration. In this case the more posterior location of the first dorsal fin may be at the cost of reducing ϕ below 0.5π. However, the body and fin form typical of sharks (Thomson and Simanek 1977) probably provides for poor acceleration performance.

In conclusion, sharks appear to have exploited their different structural capacities to specialize for cruising when swimming.

ACKNOWLEDGMENTS

This work was completed while P. W. Webb was an NRC/NOAA Research Associate on leave from the University of Michigan. I am indebted to R. Lasker and J. R. Hunter for their hospitality. The authors thank Sea World for providing specimens and facilities.

LITERATURE CITED

ALEXANDER, R. McN.
1968. Animal mechanics. Univ. Washington Press, Seattle, 346 p.
ALEYEV, Y. G.
1977. Nekton. Junk, The Hague, 435 p.
BAINBRIDGE, R.
1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. J. Exp. Biol. 35:109-133.
1963. Caudal fin and body movement in the propulsion of some fish. J. Exp. Biol. 40:23-56.
BREDER, C. M., JR.
1926. The locomotion of fishes. Zoologica (N.Y.) 4:159-297.
BRETT, J. R., AND J. M. BLACKBURN.
1978. Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. J. Fish. Res. Board Can. 35:816-821.

GRAY, J.
1933. Studies in animal locomotion. I. The movement of fish with special reference to the eel. J. Exp. Biol. 10: 88-104.

HUNTER, J. R., AND J. R. ZWEIFEL.
1971. Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus*, and other fishes. Fish. Bull., U.S. 69:253-266.

JOHNSON, C. S.
1970. Some hydrodynamic measurements on sharks. Nav. Underwater Cent. Tech. Rep. 189, 13 p.

LIGHTHILL, M. J.
1970. Aquatic animal propulsion of high hydromechanical efficiency. J. Fluid Mech. 44:265-301.
1975. Mathematical biofluiddynamics. SIAM, Phila., 281 p.

LINDSEY, C. C.
1978. Form, function, and locomotory habits in fish. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, vol. VII, p. 1-100. Acad. Press, N.Y.

NEWMAN, J. N., AND T. Y. WU.
1973. A generalized slender-body theory for fish-like forms. J. Fluid Mech. 57:673-693.

ROSEN, M. W.
1959. Water flow about a swimming fish. U.S. Navy Ordinance Test Stat. Tech. Publ. 2289, 96 p.

SPARENBERG, J. A., AND A. K. WIERSMA.
1975. On the efficiency increasing interaction of thrust producing lifting surfaces. *In* T. Y.-T. Wu, C. J. Brokaw, and C. Brennen (editors), Swimming and flying in nature, vol. 2, p. 891-917. Plenum Press, N.Y.

THOMSON, K. S., AND D. E. SIMANEK.
1977. Body form and locomotion in sharks. Am. Zool. 17:343-354.

WARDLE, C. S.
1975. Limit of fish swimming speed. Nature (Lond.) 255:725-727.

WARDLE, C. S., AND J. J. VIDELER.
1980. How do fish break the speed limit? Nature (Lond.) 284:445-447.

WEBB, P. W.
1971. The swimming energetics of trout. 1. Thrust and power output at cruising speeds. J. Exp. Biol. 55:489-520.
1973. Effects of partial caudal-fin amputation on the kinematics and metablic rate of underyearling sockeye salmon (*Oncorhynchus nerka*) at steady swimming speeds. J. Exp. Biol. 59:565-581.
1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Can. 190, 158 p.
1982. Locomotor patterns in the evolution of actinopterygian fishes. Am. Zool. 22:329-342.

WEIHS, D., R. S. KEYES, AND D. M. STALLS.
1981. Voluntary swimming speeds of two species of large carcharhinid sharks. Copeia 1981:219-222.

WU, T. Y.
1971. Hydrodynamics of swimming fishes and cetaceans. Adv. Appl. Math. 11:1-63.

POPULATION BIOLOGY OF CHUM SALMON, *ONCORHYNCHUS KETA*, FROM THE FRASER RIVER, BRITISH COLUMBIA

TERRY D. BEACHAM[1] AND PAUL STARR[2]

ABSTRACT

Population biology of Fraser River chum salmon, *Oncorhynchus keta*, was investigated. Mean age of chum salmon during the run declined from 3.98 years in October to 3.78 years in December in the 1970s. Females were more abundant than males in 4-year-old chum salmon, but males were more abundant than females in 3- and 5-year-old chum salmon. Fecundity of females was 3,250 eggs/female at a standard length of 58.0 cm and did not vary among years sampled. Fry tended to migrate downstream earlier when the previous winter had been warm than when it was cold. Egg-to-fry survival was correlated with rainfall, air temperature, and number of eggs deposited. Mean age of return of a brood year was positively correlated with its abundance. The return to escapement ratio for even-numbered brood years was inversely correlated with the abundance (catch plus escapement) of the previous brood year, which suggests that marine survival of chum salmon may be density-dependent. The return to escapement ratio for odd-numbered brood years was positively correlated with early downstream migration of chum salmon fry relative to pink salmon, *O. gorbuscha*, fry and with increased chum salmon spawning escapements relative to those of pink salmon.

Stocks of chum salmon, *Oncorhynchus keta*, in British Columbia and Alaska have fluctuated considerably in abundance (Hoar 1951; Wickett 1958; Hunter 1959; Helle 1979). These fluctuations have been attributable to variability in freshwater and marine survival, and have been related to climatic factors such as rainfall (Wickett 1958) and to population density or predation on fry (Hunter 1959). Chum salmon in British Columbia return to spawn in their natal streams mainly as 3- and 4-yr-olds, and to a lesser extent as 5-yr-olds. The mean age of returning adults tends to be greater for stocks from northern British Columbia than from southern British Columbia (Pritchard 1943; Ricker 1980). Chum salmon tend to spawn later in the fall than other species of *Oncorhynchus*, and the fry migrate downstream in the spring, within a few days after emerging from spawning beds.

The chum salmon stocks of the Fraser River have supported commercial fisheries in Johnstone Strait, the Strait of Georgia, and the Fraser River for many years (Palmer 1972) (Fig. 1). Annual catches of chum salmon were extensive in Johnstone Strait during 1951-54, ranging from 0.7 to 2.0 million fish, and in the Fraser River, ranging from 274,000 to 479,000 fish. However, the annual contribution of Fraser River chum salmon to the Johnstone Strait catch is unknown before 1964. Catches of chum salmon declined substantially during 1965-69, ranging from 23,000 to 649,000 fish in Johnstone Strait (an estimated 0 to 228,000 Fraser River chums), and 10,000 to 196,000 fish in the Fraser River. Catches have continued to vary widely in the 1970s. Fraser River chum salmon have thus shown marked fluctuations in abundance, and these fluctuations have not been satisfactorily accounted for. It is not currently possible to identify stocks of Fraser River chum salmon, so for purposes of the analysis, Fraser chum salmon were treated as a unit stock. This paper describes the population biology of Fraser River chum salmon and results of studies on the causes of variability in the number of returning adults.

MATERIALS AND METHODS

Estimates of abundance of returning adult and downstream migrating fry were derived by different sampling methods. Fry were enumerated during 1965-81 on the lower Fraser River near Mission City (Fig. 1) using techniques previously described by Todd (1966) and Bailey

---

[1] Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C., Canada V9R 5K6.

[2] Department of Fisheries and Oceans, Field Services Branch, 1090 West Pender Street, Vancouver, B.C., Canada V6E 2P1.

Manuscript accepted April 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

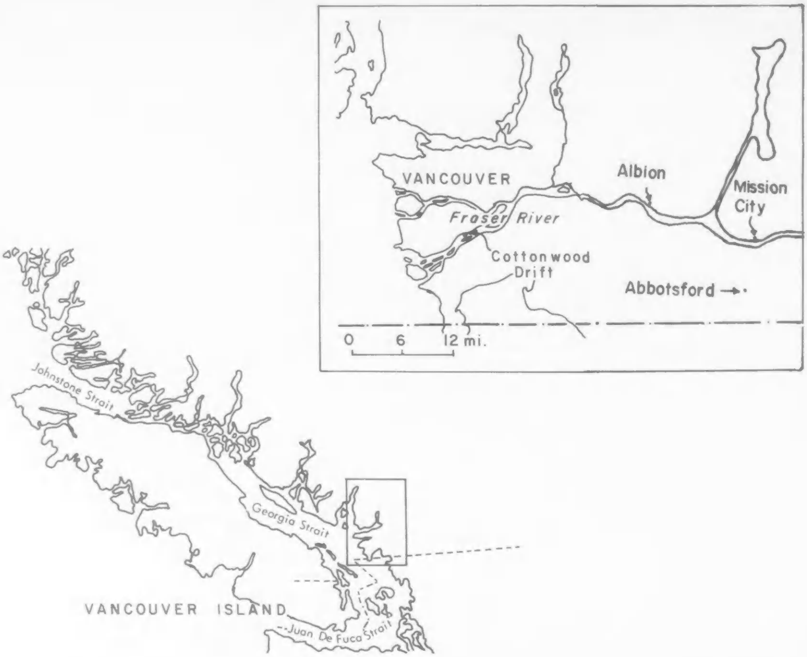


FIGURE 1.—Areas in British Columbia where Fraser River chum salmon are caught in the commercial fishery. Inset shows areas in the lower Fraser River where fry and returning adults were sampled.

(1979[3]). Briefly, the sampling procedure consisted of suspending traps at various depths from the surface to 3.7 m (12 ft) from either side of a boat travelling at a constant velocity relative to the water for 15-min periods. Samples were taken in this manner between 0500 and 1300 h. Preliminary sampling had established that chum fry migrated past Mission City were most active during this period. Sampling occurred during this period, 5 d a week from beginning of March to end of May. Daily sampling was continued for 24 h 2 or 3 d/wk so that estimates of the daily proportion of fry migrating during the standard shift (0500 to 1300 h) could be made, and daily totals of chum fry migrating past Mission City calculated. Sampling was also performed at different sites across the 527 m (1,725 ft) width of the Fraser River at Mission City. The depth and cross-sectional area of the river were known at each sampling site, as well as the area sampled by the fry traps, so that, by extrapolation, the number of fry migrating downstream daily could be estimated. Abundance of chum salmon fry used in the present analysis was taken from Bailey (footnote 3), as were the dates when 50% of the chum and pink, *O. gorbuscha*, salmon fry were estimated to have migrated past the sampling site. Weekly mean lengths (mm) of fry were determined in 1978.

Sex ratios, age composition, length-at-age, and fecundity of adult chum salmon arriving at the river mouth were derived from test fishing conducted at Cottonwood Drift from 1962 to 1979 and Albion from 1978 to 1979 (Fig. 1). A 274 m (150-fathom) long, 60-mesh deep gill net having 16.9 cm (6¾ in) mesh was set for a standard 30-min drift twice a day during the slack period of the lowest tide of the day. Smaller fish may have avoided capture on account of gill net selectivity (McCombie and Berst 1969; Todd and Larkin

---

[3] Bailey, M. D. 1979. Enumeration of salmon in the Fraser River. Unpubl. manuscr., 122 p. Department of Fisheries and Oceans.

1971), which could possibly bias adult age composition, sex ratios, and fecundity estimates. However, we believe that any bias present was not of sufficient magnitude to mask trends in abundance of individual brood years. Daily test fishing 5 d/wk was usually conducted from late September until mid-December, although sampling within this period was not conducted when the commercial fishery was operating in the river. Ages of chum salmon were determined from scales. Bilton and Ricker (1965) and LaLanne and Safsten (1969) have outlined the methodology of using scales for aging chum salmon. Lengths were recorded as either fork length or postorbital-hypural length to the nearest millimeter. Fecundity was determined by direct counts of the number of eggs in both ovaries. Age composition in the escapement was assumed to be the same as that in the test fishery. Escapement was estimated during the 1960s by visual counts on spawning beds, by test fishing, and by a tagging program (Palmer 1972), whereas in the 1970s, escapement was estimated from visual counts and test fishing only. Total returns for a brood year included the catch plus escapement.

Fraser River chum salmon are taken by the fishery which operates near the river mouth, and by fisheries in Johnstone Strait, the Strait of Georgia, and at Point Roberts in the United States. The proportion of Fraser River chum salmon in the Johnstone Strait fishery was estimated seasonally based on the tagging studies reported by Palmer (1972). Since the fishery in the Strait of Georgia exploits mixed stocks of chum salmon, it was not possible to estimate the contribution of Fraser River chum salmon in this fishery, although it is small compared with the catch in Johnstone Strait. Catches in the Fraser River, as well as 100% of the catches off Point Roberts, and the Fraser River contribution to Johnstone Strait were summed to estimate the total annual catch of Fraser River chum salmon. Although not all chum salmon caught off Point Roberts, 20 km south of the Fraser River mouth, may be bound for the Fraser River, any overestimation of the Fraser River contribution to the Point Roberts catch is compensated for by underestimation of the Fraser River contribution to the Strait of Georgia catch. Escapements of pink salmon used in the present study were those listed in the annual report of the International Pacific Salmon Fisheries Commission for 1979 (Anonymous 1980).

RESULTS

Marine Growth

High-seas scale and tagging studies have indicated that chum salmon from British Columbia and Alaska range from lat. 45°N to 60°N and from long. 130°W to 180° in the North Pacific Ocean (Shepard et al. 1968). Specific distributions of Fraser River chum salmon were not available. However, the effect of variability in ocean water temperatures on growth rate was investigated by comparing the mean monthly temperature from March through August (major part of growing season) at Station P (lat. 50°N, long. 145°W) and mean length-at-age of returning adults. Fork lengths of returning adults during 1960-69 were taken from Palmer (1972) and were converted to postorbital-hypural lengths by the regressions:

$$\text{Males: } H = 1.08\ FL - 219\ (N = 100,\ r = 0.72)$$
$$\text{Females: } H = 1.00\ FL - 130\ (N = 100,\ r = 0.89)$$

where FL = fork length in millimeters and H = postorbital-hypural length in millimeters. These regressions were derived from chum salmon taken by the Fraser River commercial fishery in 1962 and 1963. Postorbital-hypural lengths of returning adults during 1970-78 were derived from the test fishery at Cottonwood Drift. For the period of 1960-78, mean lengths-at-age of 4-yr-old chum salmon were correlated with water temperature at Station P during the penultimate growing season for males ($r = 0.49$, $n = 19$, $P<0.05$) and females ($r = 0.44$, $n = 19$, $P<0.06$). However, there was no correlation for mean length-at-age and water temperature at Station P during the penultimate growing season for age-3 fish (males: $r = 0.17$, $n = 19$, $P>0.10$; females: $r = -0.08$, $n = 19$, $P>0.10$) or in the year of return and mean length-at-age for age-3 fish (males: $r = 0.17$, $P>0.10$; females: $r = 0.10$, $P>0.10$). The relatively stable mean length-at-age for returning age-3 chum salmon is undoubtedly due to selectivity of the sampling gear, with possibly only the larger age-3 fish susceptible to capture in a 16.9 cm mesh gill net.

Age Composition and Sex Ratios of Returning Adults

The mean monthly age composition of chum salmon migrating upstream during the years

1970-79 indicated that the proportion of age-5 fish in the run decreased from October through December, whereas the proportion of age-3 fish increased (Table 1). Age-4 chum salmon comprised about 74% of the run in each month, while age-3 comprised 24% of the run in December but only 14% in October.

Sex ratios were variable among ages, with more male chum salmon returning at age 3 ($X^2 = 23.7$, df = 1, $P<0.01$) and age 5 ($X^2 = 10.7$, $P<0.01$) than did females (Table 2). More female chum salmon returned at age 4 than did males ($X^2 = 70.6$, $P<0.01$). Since the mean age of chum salmon in the run decreased through time, and sex ratios vary with age, the sex ratio of the run may also vary through time. However, an application of the sex ratios by age in Table 2 to the age compositions in Table 1 shows that sex ratios of the total run were nearly the same each month (52.9% females in October, 53.1% in November, and 52.9% in December).

TABLE 1.—Percentage age composition by month (October-December) of chum salmon sampled in the Fraser River test fishery, 1970-79. Sample sizes are in parentheses.

Age	October	November	December
3	13.7 (326)	21.7 (715)	23.8 (307)
4	74.3 (1,826)	74.3 (2,443)	73.4 (947)
5	12.0 (304)	4.0 (132)	2.6 (36)
Total	100.0 (2,456)	100.0 (3,290)	100.0 (1,290)
Mean age (yr)	3.98	3.82	3.78

TABLE 2.—Sex ratios (males:females) of age-3, -4, and -5 chum salmon sampled in the Fraser River test fishery, 1960-79.

Age:	3	4	5
Ratio	1.19	0.79	1.30
Sample size	3,172	5,378	626

Fecundity

Fecundity was determined from samples of chum salmon taken in 1966, 1968, and 1978 with females ranging in postorbital-hypural length from 50 to 66 cm. Females sampled in 1978 were generally larger than those in 1966 and 1968 (Table 3). A two-way analysis of covariance with sampling year and age as factors and length as a co-variate (co-variate was accounted for before factors were tested) indicated that there was no significant difference in fecundity (F) among years ($F=0.92$, df = 2 and 228, $P>0.05$) or among ages ($F = 2.66$, $P>0.05$). The mean fecundity for all samples was 3,250 eggs/female (Table 3).

The relationship between fecundity and length of 234 females sampled was described by:

$$\log_e F = 2.8659 + 0.8193 \log_e L \ (r = 0.29) \quad (1)$$

where F = fecundity and L = postorbital-hypural length in millimeters. The regression was significant ($F = 20.1$, $P<0.01$), but accounted for about only 9% of the variability in fecundity (Fig. 2). Most of the females sampled were between 54 and 63 cm in length, and with high variability in fecundity within this short length range, little of the variability in fecundity could be accounted for by the regression.

TABLE 3.—Number of females sampled, mean length (cm), mean age (yr), and mean fecundity of chum salmon from the Fraser River. SE = standard error of mean.

Year:	1966	1968	1978	Total
n	109	76	49	234
Length	57.4	57.9	59.5	58.0
SE of length	0.2	0.3	0.4	0.2
Age	3.90	3.89	3.90	3.90
Fecundity	3,227	3,276	3,261	3,250
SE of fecundity	39.5	46.6	60.1	27.7
Age:	3	4	5	
n	26	194	2	
Length	55.8	58.1	58.3	
SE of length	0.6	0.2	1.3	
Fecundity	3,292	3,246	3,091	
SE of fecundity	83.6	28.4	287.9	

Fry Migrations and Survival

The major portion of the downstream migration of chum salmon fry passed the Mission City sampling site from mid-March to the end of April. Usually 50% of the fry had passed the sampling site between April 13th and the 23d (Fig. 3), although 50% of the fry have passed the sampling site as early as April 3 (1976 brood year) and as late as May 3 (1971 brood year). About 80% of the chum salmon fry migrate downstream at a length of <40 mm. However, the proportion of fry >40 mm long during the downstream migration tends to increase with time. By the second week of May 1978, 20% of the fry were >43 mm long and weighed 1.0 g, which suggests a period of freshwater rearing for these fry.

Linear regression was used to determine the relationship of air temperature (T), determined as the mean of monthly air temperatures at the Abbotsford airport from December through February, to timing of the fry migration (F),

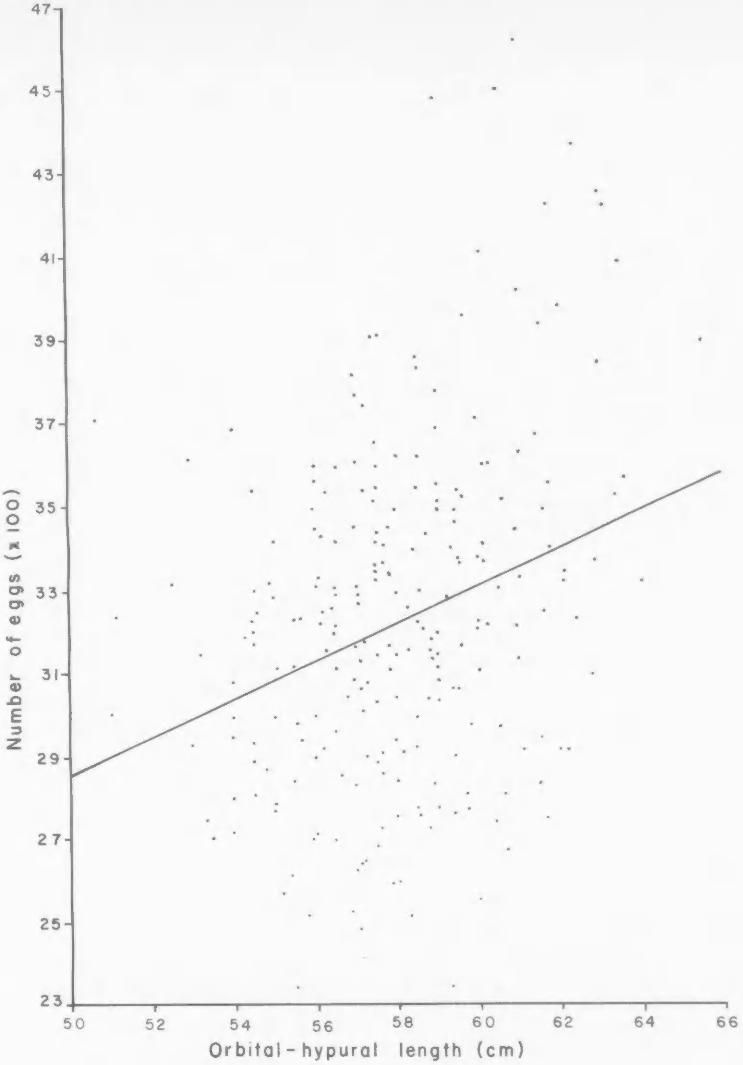


FIGURE 2.—The relationship between fecundity and length in female chum salmon sampled from the test fishery in 1966, 1968, and 1978.

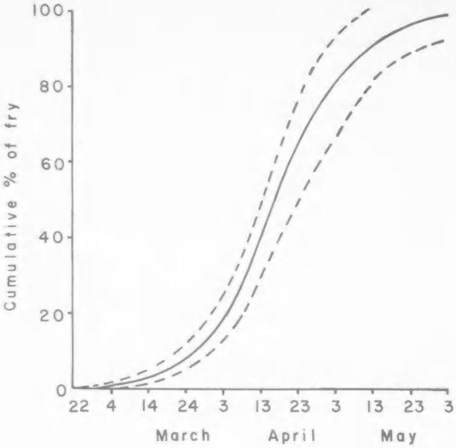


FIGURE 3.—Mean time of chum fry downstream migrations on the Fraser River, 1965-80. Dotted lines indicate 95% confidence limits.

measured as the days from April 1 to the date of 50% migration. Abbotsford airport is located near many major chum salmon spawning areas (Fig. 1). The model fitted was:

$$F = \frac{25.53}{T^{0.444}} \ (n = 15) \qquad (2)$$

and the regression was significant ($r = 0.61$, $P<0.05$) (Fig. 4). Fry tend to migrate downstream earlier following a warmer winter than following a colder winter, presumably because warmer temperatures accelerate egg development.

Based on estimates of the number of migrating fry and egg deposition (Table 4), egg-to-fry survival varied from 6% to about 35% in the 1961-78 brood years. Multiple regression was used to determine the relationship of rainfall, egg numbers, air temperature, and their interactions on variability in egg survival. The model fitted through stepwise regression was:

$$S = a\,T + b\,T \times \frac{1}{R} + c\,T \times \frac{1}{E} + d\,T \times \frac{1}{R} \times \frac{1}{E} + e \qquad (3)$$

where S = % egg to fry survival

T = mean monthly air temperature at Abbotsford airport from December through February

R = total rainfall in cm at Abbotsford airport from November through January

E = number of eggs deposited $\times 10^6$.

The analysis yielded:

Variable	*Coefficient*	*SE*	*t*
T	−7.62	2.51	−3.03
T/R	615.90	130.42	4.72
T/E	4,369.52	1,375.07	3.18
T/RE	−266,517.54	77,530.32	−3.44
Constant	5.99		

The regression was significant ($R^2 = 0.77$, $F = 10.75$, df = 4 and 13, $P<0.01$), and the correlation matrix for the model is shown in Table 5. The individual factors of rainfall ($r = -0.28$) and egg numbers ($r = -0.005$) were not significantly correlated with egg survival, but their interactions with temperature were. Egg survival tended to increase during drier winters, but if these drier winters were also relatively cold, then egg survival was lowered. If the winter was both relatively dry and warm, then egg survival was good, as was the case for the 1976 brood year (Table 4).

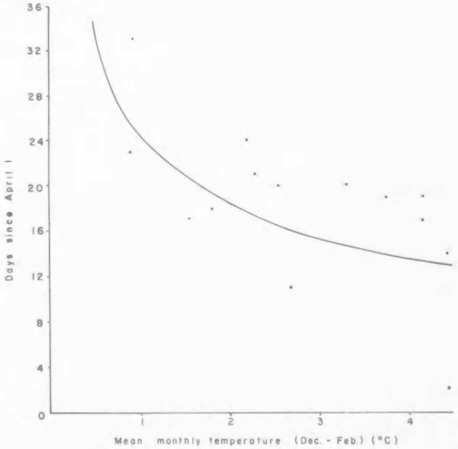


FIGURE 4.—Median date of downstream chum fry migration versus mean monthly temperature from December through February as measured at the Abbotsford airport.

TABLE 4.—Escapements, survivals, returns-at-age, mean age of return, and return to escapement ratios of Fraser River chum salmon, 1961-74 brood year. Percentage age composition for each brood year is in parentheses.

Brood year	Spawning escapement	No. of females	Egg deposition ($\chi10^6$) at 3,250/female	No. of fry ($\chi10^6$)	% egg to fry survival	Adult returns ($\chi10^3$)	% fry to adult survival	Return at age ($\chi10^3$) 3 yr	4 yr	5 yr	Mean age of return (yr)	Total return ($\chi10^3$)	Return to escapement
1961	164,000	83,800	272.4	25.8	9.5	236.3	0.91	98.6 (41.7)	132.0 (55.9)	5.7 (2.4)	3.61	236.3	1.44
1962	180,000	90,000	292.5	42.5	14.5	468.1	1.10	63.4 (13.5)	396.5 (84.7)	8.2 (1.8)	3.88	468.1	2.60
1963	214,000	107,000	347.8	54.8	15.8	178.2	0.33	50.7 (28.5)	123.6 (69.4)	3.9 (2.1)	3.74	178.2	0.83
1964	325,000	135,850	441.5	53.6	12.1	1,293.9	2.41	171.2 (13.2)	1,108.7 (85.7)	14.0 (1.1)	3.88	1,293.9	3.98
1965	185,000	109,930	357.3	32.4	9.1	579.8	1.79	211.9 (36.6)	363.9 (62.7)	4.0 (0.7)	3.64	579.8	3.13
1966	430,000	236,500	768.6	75.2	9.8	925.8	1.23	257.3 (27.8)	627.0 (67.7)	41.5 (4.5)	3.77	925.8	2.15
1967	212,000	102,600	333.5	69.0	20.7	325.4	0.47	53.5 (16.4)	224.5 (69.0)	47.4 (14.6)	3.98	325.4	1.53
1968	822,000	392,910	1,277.0	72.5	5.7	1,933.9	2.67	146.0 (7.6)	1,549.9 (80.1)	238.0 (12.3)	4.05	1,933.9	2.35
1969	390,100	206,360	670.7	107.4	16.0	1,434.6	1.34	58.5 (4.1)	1,174.4 (81.9)	201.7 (14.0)	4.10	1,434.6	3.68
1970	303,100	175,500	570.4	48.7	8.5	534.2	1.10	47.9 (9.0)	477.7 (89.4)	8.6 (1.6)	3.93	534.2	1.76
1971	356,700	142,980	464.7	58.2	12.5	367.7	0.63	161.0 (43.8)	200.7 (54.6)	6.0 (1.6)	3.58	367.7	1.01
1972	579,700	333,330	1,083.3	109.5	10.1	1,239.1	1.13	242.8 (19.6)	984.4 (79.4)	11.9 (1.0)	3.82	1,239.1	2.14
1973	453,000	250,510	814.2	130.8	16.1	653.0	0.50	205.7 (31.5)	427.5 (65.5)	19.8 (3.0)	3.72	653.0	1.42
1974	565,300	291,130	946.2	114.4	12.1	1,210.5	1.06	136.7 (11.3)	1,022.6 (84.5)	51.2 (4.2)	3.93	1,210.5	2.16
1975	235,300	125,890	409.1	73.0	17.8			158.9	227.4				
1976	588,700	310,830	1,010.2	358.2	35.4			96.7					
1977	538,800	271,020	880.8	124.3	14.1								
1978	486,600	268,603	873.0	88.1	10.1								
1979	327,700	173,700	564.5	109.4	19.4								

TABLE 5.—Correlation matrix for the egg-to-fry survival model. Variables are listed in the text.

	Variable S	T	T/R	T/E	$T/E \times R$
S	1.00	0.52	0.73	0.22	0.29
T		1.00	0.80	0.66	0.60
T/R			1.00	0.49	0.64
T/E				1.00	0.93
$T/E \times R$					1.00

There was a slight tendency for egg survival to decline with increasing numbers of eggs deposited and this effect was enhanced by a cold winter. Thus spawning escapement (egg deposition), rainfall, and temperature interact to produce variable freshwater survival. Fry-to-adult survival was inversely correlated with egg-to-fry survival ($r = -0.62$, $n = 14$, $P<0.05$), which suggests a density-dependent response of chum salmon fry survival.

Age of Return

Total returns from the 1961 through the 1974 chum salmon brood years have ranged from 180,000 to 1,930,000 fish (Table 4). The proportion of the brood year returning at age 3 has ranged from 4% to about 42%. To determine if the mean age at maturity from a brood year was dependent upon the total number of adults produced from that brood year, we regressed mean age at maturity (in years) on total return (Fig. 5). This regression produced:

$$\text{Mean age} = 3.67 + 1.923 \times 10^{-7}\ \text{Returns} \quad (n = 14) \qquad (4)$$

where $r = 0.63$ ($P<0.05$). The mean age at maturity of a brood year increased as did the total num-

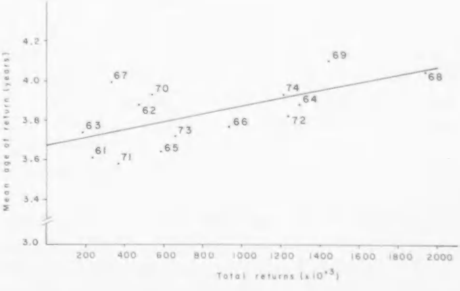


FIGURE 5.—Mean age of return of a brood year of chum salmon versus its abundance.

ber of returning adults, which suggests that if the timing of returns is size dependent, then density-dependent growth may occur during the ocean residence of chum salmon. Pink salmon return to the Fraser River in abundance in odd years, but return in negligible amounts in even years. The mean age at maturity and number of returning chum salmon adults tended to be higher in even brood years than in odd ones (Fig. 5), so that pink salmon may indirectly influence mean age at maturity of chum salmon through an effect on survival of chum salmon.

The proportion of a brood year returning at age 3, 4, and 5 is frequently of importance in predicting annual returns. For Fraser River chum salmon, the percentage age composition of the returns from a brood year is related to the mean age of return of the brood year as follows:

$$\%\ \text{age } 3 = 321.56 - 78.26 \text{ mean age} \quad (r^2 = 0.93) \qquad (5)$$

$$\%\ \text{age } 4 = -141.68 + 56.20 \text{ mean age} \quad (r^2 = 0.63) \qquad (6)$$

$$\%\ \text{age } 5 = -79.88 + 22.06 \text{ mean age} \quad (r^2 = 0.50). \qquad (7)$$

If the returns from a brood year can be predicted, then the mean age of return of a brood year can be obtained from Equation (4) and applied to Equations (5)-(7) in order to obtain numbers returning at each age.

Return to Escapement

The ratio of total returns for a brood year to escapement (*R/S*) has varied from 0.8 to 4.0 for the 1961 through 1974 brood years. The available evidence suggests that for escapements below 850,000 adults, egg-to-fry and fry-to-adult survivals will generally be large enough to allow the number of returning chum salmon to remain above replacement levels (Fig. 6). However, only the 1968 escapement was above 600,000 adults, so further information on the *R/S* ratio for escapements >500,000 adults is required in order to evaluate the effect of varying escapements on chum salmon survival. There was no evidence to indicate a decline in recruits per spawner at escapements >500,000 fish, and thus the optimal escapement is uncertain. Optimal escapements will not be established with confidence until declines in recruits per spawner (or density-dependent mortality) is observed at high spawning stock sizes.

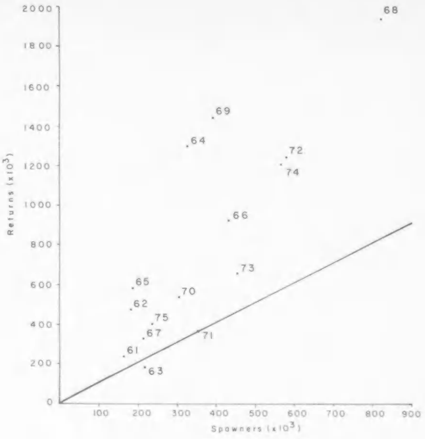


FIGURE 6.—Total return versus numbers of spawners for the 1961-75 brood years of Fraser River chum salmon.

Fry-to-adult survival has been variable, ranging from 0.3% to 2.4% (Table 4). The average survival for the even brood years was 1.53%, whereas survival for the odd brood years was 0.85%. The effect of fry abundance on variability in fry-to-adult survival was investigated for odd brood years by summing the estimated numbers of chum salmon and pink salmon fry, and for even brood years by assuming that the number of pink salmon fry produced was negligible. The data suggested that chum salmon fry survival tended to increase when the abundance of chum and pink salmon fry decreased (Fig. 7). This relationship can be expressed by:

$$\%\ \text{survival} = 0.73 + \frac{46.53}{\text{Fry abundance (millions)}} \qquad (r = 0.52) \qquad (8)$$

for the 1961-75 brood years. All of the fry-to-adult survivals for the odd brood years, except for the 1965 and 1969 brood years, were below 1.0%, whereas all of the fry-to-adult survivals for the even brood years were above 1.0%, with the 1964 and 1968 brood year fry survival being higher than the rest.

Some of the variability in fry-to-adult survival was due to the timing of the downstream fry migration. The higher survival of the 1965 and 1969 brood year fry when compared with other odd

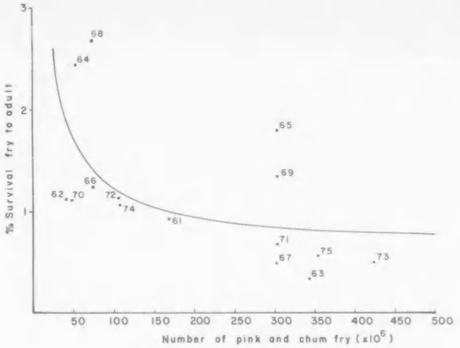


FIGURE 7.—Fry-to-adult survival for chum salmon versus total abundance of pink and chum salmon fry. The abundance of pink fry from even-numbered brood years was assumed to be negligible.

brood years may be accounted for by the early downstream migration, and the same condition may apply to even brood years (Fig. 8).

With fry-to-adult survivals of Fraser River chum salmon generally lower in odd brood years than in even ones, odd- and even-numbered brood years were separated in a further analysis of variability in the returns to spawners relationship. The R/S ratio for even brood years was inversely related with the total number of returning adults of the previous odd brood year (Fig. 9). This relationship was determined through regression and is described by:

$$\frac{R_t}{S_t} = 1.367 + \frac{0.3867}{R_{t-1}} \quad (n = 7) \tag{9}$$

where R_t = total returns for even-numbered brood year

S_t = spawning escapement producing that brood year

R_{t-1} = total returns of previous brood year in millions

and the correlation between R_t/S_t and $1/R_{t-1}$ was significant ($r = 0.91$, $P<0.01$). This equation can be rearranged to give a prediction of total number of returning adults in year t, given escapement and total return of the previous brood year. The above suggests that survival of chum salmon in the marine environment is dependent upon the abundance of conspecifics in the previous brood year. Marine survival may thus be density-dependent, and interbrood year interactions, possibly through competition for food, may affect marine survival of chum.

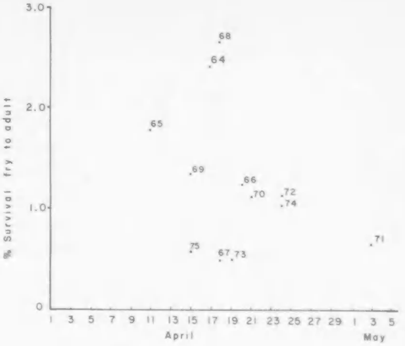


FIGURE 8.—Fry-to-adult survival of chum salmon versus median date of downstream migration.

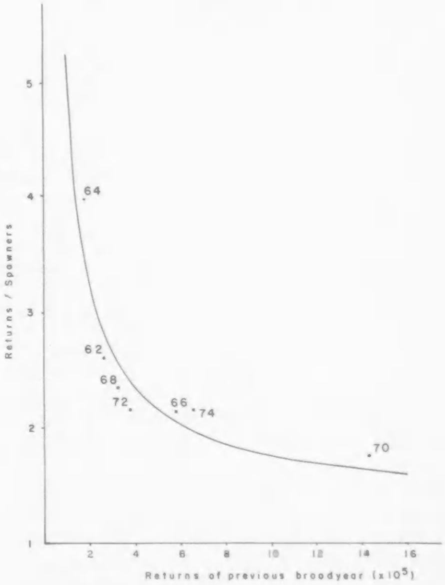


FIGURE 9.—Ratio of returns/spawners for even-numbered brood years of Fraser River chum versus chum abundance in previous brood year.

Pink salmon have been implicated in the present study as impacting population dynamics of Fraser River chum salmon during odd brood years. Multiple regression was used to describe the effect of pink salmon on chum salmon fry survivals by:

$$\frac{R}{\mathrm{S}} = a\,\frac{S}{\mathrm{P}} + b(D) + c \qquad (10)$$

where R = total returns from a given brood year
S = spawning escapement of chum salmon that produced a given brood year
P = spawning excapement of pink salmon in same brood year
D = median time of downstream pink salmon fry migration minus median for chum salmon fry in days
c = regression constant.

The analysis yielded:

Variable	*Coefficient*	*SE*	*t*
S/P	13.268	4.928	2.69
D	0.136	0.034	3.93
Constant	−1.469		

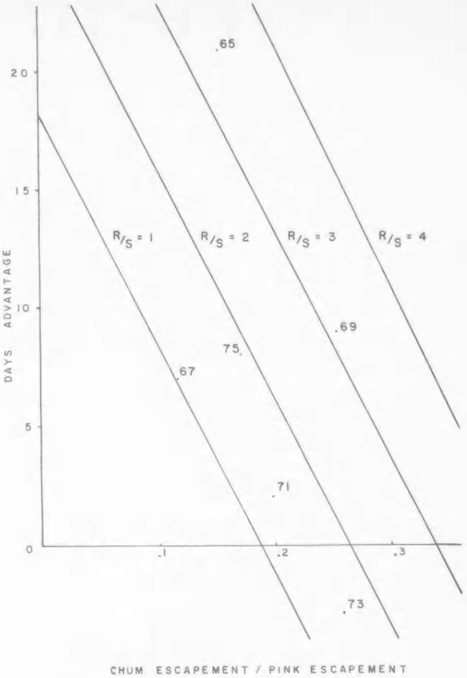


FIGURE 10.—Contour plot for returns/spawners for odd-numbered brood years of Fraser River chum in relation to timing of pink and chum fry migrations and relative spawning escapements of pink and chum. Contour lines of R/S = 1.0, 2.0, 3.0, and 4.0 are plotted.

The regression was significant ($F = 9.60$, df = 2, and 3, $P<0.05$) and accounted for 85% of the variation in R/S in odd brood years ($R = 0.92$). The chum salmon R/S ratio increases the earlier that chum salmon fry migrate downstream relative to pink salmon fry (Table 6). If chum salmon escapement is 10% of that of pink salmon, then the time of the median downstream migration of chum salmon fry must be at least 9 d earlier than that of pink salmon fry if the chum salmon spawners are just to replace themselves (R/S = 1.0) (Fig. 10). However, if chum salmon escapement is 30% of the pink salmon escapement and chum salmon fry still have a 9-d advantage over pink salmon fry, then the R/S ratio for chum salmon will be between 3.0 and 4.0, as happened for the 1969 brood year (Fig. 10). The chum salmon R/S ratio will still be between 3.0 and 4.0 if the chum salmon escapement is 15% of the pink salmon escapement, provided the chum salmon fry have at least a 19-d advantage over the pink salmon fry, similar to the 1965 brood year (Fig. 10).

TABLE 6.—Dates when 50% of the fry were estimated to have migrated downstream and estimated spawning escapements for odd-numbered brood years, 1965-77.

Brood year	Date of 50% fry migration		Spawning escapements ($x10^3$)	
	Chum	Pink	Chum	Pink
1965	11 April	2 May	185.0	1,191.1
1967	17 April	24 April	212.0	1,831.4
1969	15 April	24 April	390.0	1,529.5
1971	3 May	5 May	356.7	1,803.8
1973	19 April	16 April	453.0	1,754.1
1975	15 April	23 April	235.3	1,367.3
1977	20 April	25 April	538.8	2,387.8

DISCUSSION

Mean lengths at maturation for 4-yr-old chum salmon in the present study were found to be significantly correlated with oceanic water temperatures in the penultimate growing season but not in the final one. Helle (1979) found that oceanic environmental factors during the final ocean year strongly influenced length at maturity of chum salmon from Olsen Creek, Alaska. The causes of the different results of the two studies are uncertain, but may in some way be related to the timing of the attainment of a threshold length for spawning.

The fecundity of Fraser River chum salmon (3,250 eggs/female) reported in the present study was greater than that reported by Foerster and Pritchard (1936) for Fraser River chum salmon (2,943 eggs/female), for Nile Creek chum salmon (2,726 eggs/female) (Neave 1953), and for Hooknose Creek chum salmon (2,083-3,097 eggs/female) (Hunter 1959). Only a few of the mean fecundities listed by Bakkala (1970) for North American and Asian chum salmon were greater than that of Fraser River chum salmon. However, size and age compositions of chum salmon sampled for fecundity in the former studies were unavailable, and it may be that larger sized chum salmon were sampled in the Fraser than in other areas because smaller females may have avoided the test fishery.

In chum salmon, males have been reported to predominate in the early part of the run and females in the later part (Gilbert 1922; Henry 1954). In the present study, sex ratios as measured by the test fishery remained relatively constant during the fall upriver migration. This result was probably due to differences in run timing of stocks in the Fraser River, so that stocks in different stages of completeness of the run were sampled at the same time, and thus temporal shifts in sex ratios may have been obscured.

Freshwater and marine survival of Fraser River chum salmon have varied about sixfold and fivefold, respectively. Rainfall and gravel permeability have been implicated in variable freshwater survival elsewhere, with higher rainfall in the fall (except in flood years) and looser, more permeable gravel resulting in higher survival (Wickett 1958). Freshwater survival of chum salmon in Hooknose Creek was inversely related to the total number of pink and chum salmon eggs deposited (Hunter 1959). The present study indicated that freshwater survival of Fraser River chum salmon was inversely related to the amount of winter rainfall, and that much of the variability in freshwater survival was attributable to interactions among temperature, rainfall, and egg abundance.

Mortality among young fry has been suggested to be a major influence in determining the abundance of returning adults from a brood year of pink or chum salmon (Neave 1953; Hunter 1959; Parker 1965). Egg-to-fry survival in Fraser River chum salmon was largely dependent upon physical environmental fluctuations, whereas fry-to-adult survival may be dependent upon chum and pink salmon abundance. The effects of favorable or unfavorable environmental conditions during incubation appear to be compensated for by density-dependent responses of survival during the marine life history stage of chum salmon. Density-dependent survival during the marine residence period has been suggested for several *Oncorhynchus* species, with possible interactions within and among brood years (Peterman 1978). The present study indicated that for even brood years of Fraser River chum salmon, marine survival may be inversely associated with the abundance of the previous brood year, which suggests that the number of returns from a brood year is not determined until the mixing of underyearlings and older chum salmon in the ocean. Although early fry mortality is undoubtedly heavy in chum salmon, as it is in other marine fish, and although it has been suggested that the determination of year-class abundance occurs soon after hatching in marine fishes (Cushing and Harris 1973), some evidence does suggest that year-class abundance is not determined in the first year of life of marine fishes (Ponomarenko 1973; Lett et al. 1975).

The present study indicated that the mean age of returns of a brood year increased with brood year abundance. Similar observations have been reported by Birman (1951) for chum salmon in the Amur River in the Soviet Union and Helle (1979) for chum salmon in Olsen Creek in Alaska. This result implies that growth during ocean residence is density-dependent, as has been reported in other marine fishes (Sonina 1965; Paloheimo and Kohler 1968; Templeman et al. 1978). Competition for food may be one of the mechanisms of this density-dependence. The present study also indicated that higher marine water temperatures were accompanied by increased growth rates, as indicated by annual variability in size of returning 4-yr-old chum salmon.

The present study suggests that there may be competition between chum and pink salmon fry in the Fraser River estuary or Strait of Georgia. Phillips and Barraclough (1978) found that chum salmon fry in the Strait of Georgia near the Fraser estuary were larger in 1967 and 1969 when pink salmon fry abundance would be low than those in 1966 and 1968 when pink salmon fry would be abundant. When chum and pink salmon fry migrated at similar times, chum salmon fry-to-adult survival was lower than when chum salmon fry migrated earlier than pink salmon fry. Pink salmon grow faster than do chum salmon (Ricker 1964), and this faster growth rate may allow them to outcompete chum salmon fry for food. The influence of pink salmon on egg-to-fry survival of chum salmon was not examined, but we expect it would be minimal relative to environmental influences as pink salmon spawn earlier in the Fraser River than do chum salmon.

The present study suggests some areas that need to be explored further. Interspecific interactions between pink and chum salmon fry may be investigated by marking and varying the size and time of release of chum salmon fry in years when pink salmon fry are present and measuring rates of adult returns for these sets of fry, similar to the studies of Fraser et al. (1978) for chum on the Big Qualicum River and Bilton (1978) for coho salmon, *Oncorhynchus kisutch.*

ACKNOWLEDGMENTS

We are indebted to those who sampled and aged the salmon caught in the test fishery and sampled the fry during their downstream migrations. Tom Bilton provided the data used to convert chum fork lengths to postorbital-hypural length. M. C. Healey and B. E. Riddell made many helpful suggestions which improved the manuscript. The manuscript was prepared with the assistance of the staff at the Pacific Biological Station.

LITERATURE CITED

ANONYMOUS.
1980. Annual report 1979. International Pacific Salmon Fisheries Commission, New Westminster, B.C., 57 p.

BAKKALA, R. G.
1970. Synopsis of biological data on the chum salmon, *Oncorhynchus keta* (Walbaum) 1792. U.S. Fish Wildl. Serv., Circular 315, 89 p.

BILTON, H. T.
1978. Returns of adult coho salmon in relation to mean size and time of release of juveniles. Fish. Mar. Serv. Tech. Rep. 832, 73 p.

BILTON, H. T., AND W. E. RICKER.
1965. Supplementary checks on the scales of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). J. Fish. Res. Board Can. 22:1477-1489.

BIRMAN, I. B.
1951. (Qualitative characteristics of the stocks and dynamics of abundance of autumn chum salmon of the Amur River.) Izv. Tikhookean. Nauchno-Issled. Inst. Morskogo Rybn. Khoz. Okeanogr. (TIRNO) 35:17-31. Fish. Res. Board Can., Transl. Ser. 103.

CUSHING, D. H., AND J. G. K. HARRIS.
1973. Stock and recruitment and the problem of density dependence. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:142-155.

FOERSTER, R. E., AND A. L. PRITCHARD.
1936. The egg content of Pacific salmon. Biol. Board Can., Prog. Rep. Pac. Biol. Stn. 28:3-5.

FRASER, F. J., D. D. BAILEY, AND M. J. WOOD.
1978. Big Qualicum River salmon development project (Vol. III): Experimental rearing of chum salmon juveniles (*Oncorhynchus keta*) in fresh water (1968-1970). Fish. Mar. Serv. Tech. Rep. 752, 22 p.

GILBERT, C. H.
1922. The salmon of the Yukon River. U.S. Bur. Fish., Bull. 38:317-332.

HELLE, J. H.
1979. Influence of marine environment on age and size at maturity, growth, and abundance of chum salmon, *Oncorhynchus keta* (Walbaum), from Olsen Creek, Prince William Sound, Alaska. Ph.D. Thesis, Oregon State Univ., Corvallis, 129 p.

HENRY, K. A.
1954. Age and growth study of Tillamook Bay chum salmon (*Oncorhynchus keta*). Fish Comm. Oreg., Contrib. 19, 28 p.

HOAR, W. S.
1951. The chum and pink salmon fisheries of British Columbia, 1917-1947. Fish. Res. Board Can., Bull. 90, p. 1-46.

HUNTER, J. G.
1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16:835-886.

LALANNE, J. J., AND G. SAFSTEN.
1969. Age determination from scales of chum salmon (*Oncorhynchus keta*). J. Fish. Res. Board Can. 26:671-681.

LETT, P. F., A. C. KOHLER, AND D. N. FITZGERALD.
1975. Role of stock biomass and temperature in recruitment of southern Gulf of St. Lawrence Atlantic cod, *Gadus morhua*. J. Fish. Res. Board Can. 32:1613-1627.

MCCOMBIE, A. M., AND A. H. BERST.
1969. Some effects of shape and structure of fish on selectivity of gillnets. J. Fish. Res. Board Can. 26:2681-2689.

NEAVE, F.
1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Board Can. 9:450-491.

PALMER, R. N.
1972. Fraser River chum salmon. Can. Fish. Serv., Pac. Reg., Tech. Rep. 1972-1, 284 p.

PALOHEIMO, J. E., AND A. C. KOHLER.
1968. Analysis of the southern Gulf of St. Lawrence cod population. J. Fish. Res. Board Can. 25:555-578.

PARKER, R. R.
1965. Estimation of sea mortality rates for the 1961 brood-year pink salmon of the Bella Coola area, British Columbia. J. Fish. Res. Board Can. 22:1523-1554.

PETERMAN, R. M.

1978. Testing for density-dependent marine survival in Pacific salmonids. J. Fish. Res. Board Can. 35:1434-1450.

PHILLIPS, A. C., AND W. E. BARRACLOUGH.

1978. Early marine growth of juvenile Pacific salmon in the Strait of Georgia and Saanich Inlet, British Columbia. Fish. Mar. Serv. Tech. Rep. 830, 19 p.

PONOMARENKO, V. F.

1973. On a probable relation between age composition and spawning stock and abundance of the year classes of cod in the Barents Sea. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 164:69-72.

PRITCHARD, A. L.

1943. The age of chum salmon taken in the commercial catches in British Columbia. Fish. Res. Board Can., Prog. Rep., Pac. Coast Stn. 54:9-11.

RICKER, W. E.

1964. Ocean growth and mortality of pink and chum salmon. J. Fish. Res. Board Can. 21:905-931.

1980. Changes in the age and size of chum salmon (*Oncorhynchus keta*). Can. Tech. Rep. Fish. Aquat. Sci. 930, 99 p.

SHEPARD, M. P., A. C. HARTT, AND T. YONEMORI.

1968. Salmon of the North Pacific Ocean—Part VIII. Chum salmon in offshore waters. Int. North Pac. Fish. Comm., Bull. 25, 69 p.

SONINA, M. A.

1965. Relationship between the growth rate and population density of haddock in the Barents Sea. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6:565-570.

TEMPLEMAN, W., V. M. HODDER, AND R. WELLS.

1978. Age, growth, year-class strength, and mortality of the haddock, *Melanogrammus aeglefinus*, on the southern Grand Bank and their relation to the haddock fishery of this area. Int. Comm. Northwest Atl. Fish. Res. Bull. 13:31-52.

TODD, I. S.

1966. A technique for the enumeration of chum salmon fry in the Fraser River, British Columbia. Can. Fish Cult. 38:3-35.

TODD, I. S., AND P. A. LARKIN.

1971. Gillnet selectivity on sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) of the Skeena River system, British Columbia. J. Fish. Res. Board Can. 28:821-842.

WICKETT, W. P.

1958. Review of certain environmental factors affecting the production of pink and chum salmon. J. Fish. Res. Board Can. 15:1103-1126.

TROPHIC PATTERNS AMONG LARVAE OF FIVE SPECIES OF SCULPINS (FAMILY: COTTIDAE) IN A MAINE ESTUARY

JOANNE LYCZKOWSKI LAROCHE[1]

ABSTRACT

The food habits and trophic relationships of larvae of five species of marine cottids—*Myoxocephalus aenaeus, M. octodecemspinosus, M. scorpius, Triglops murrayi*, and *Hemitripterus americanus*—were examined and compared during winter and early spring when they cooccur at peak abundance in the Damariscotta River estuary, Maine. Overall feeding incidence was high with <14% of the larvae in any species having empty guts. Larvae of all five species began to feed before yolk absorption was complete.

Among the five species, *M. aenaeus* and *M. octodecemspinosus* were most similar in mouth size, prey size, and dominant prey—adult *Microsetella norvegica* in January and February (winter) and *Balanus* nauplii in March (early spring). Mouth size, prey size, and dominant prey in early spring (*Balanus* nauplii) of *Myoxocephalus scorpius* were similar to the other species of *Myoxocephalus*, but the most frequently ingested prey in winter was the centric diatom, *Coscinodiscus* sp. *Triglops murrayi* larvae had relatively larger mouths and ingested somewhat larger prey than similar-sized *Myoxocephalus* larvae, feeding primarily on adult *Pseudocalanus minutus* in both winter and early spring. Although mouth sizes of *H. americanus* and *T. murrayi* larvae were similar, the diet of *H. americanus* was composed almost exclusively of fish larvae, primarily other cottids.

The high incidence of ingestion of *Balanus* nauplii by *Myoxocephalus* and *T. murrayi* in early spring may indicate some degree of density-dependent food utilization by those larvae. Yet other prey, adult *Temora longicornis* and epibenthic harpacticoid copepods, appeared to be preferred over other presumably more abundant zooplankton.

Percent diet overlap was greatest among the three species of *Myoxocephalus* and, except between *M. aenaeus* and *M. octodecemspinosus*, was lower in winter when mean plankton volume (an approximate measure of food supply) was low. Observed differences in vertical distribution resulting in partial spatial segregation of *M. aenaeus* and *M. octodecemspinosus* larvae may reduce competition for food between the two species, thus allowing the consistently high degree of dietary overlap between them.

Prey size (maximum carapace width) at first feeding ranged from 100 to 375 μm among the three species of *Myoxocephalus* and >800 μm for *H. americanus*. There was no dramatic change in prey types or sizes with increasing larval size. Larvae of the five species of cottids were found to most closely resemble hake (genus *Merluccius*) in prey size relationships.

There have been relatively few detailed descriptions of the food habits of marine fish larvae despite the reputed importance of starvation as a primary cause of mortality in the sea (Hunter 1976). Our generalized concept of early feeding ecology in marine fishes is based mostly on highly fecund species whose larvae hatch from small planktonic eggs at 2-3 mm in length with undeveloped eyes and mouths (Arthur 1976; Last 1978a, b; Sumida and Moser 1980). Little is known of trophic relations among larvae of fishes such as the cottids which deposit relatively few, large, demersal eggs and whose planktonic larvae hatch at sizes ≧5 mm, in a relatively advanced stage of development with pigmented eyes and functional mouths (Laroche 1980). Fishes with widely divergent ontogenies would be expected to also have different early trophic relations, whose comparisons may yield further insights into processes controlling survival in the sea.

The kinds of food used in most laboratory studies of foraging behavior, feeding efficiencies, and growth of fish larvae are usually organisms which are easily cultured in quantity but are not natural larval fish prey, or which are known size fractions of wild plankton whose species composition is only approximately known. Laboratory results, based solely on unnatural and/or single prey, or prey described by size only, may have little relevance to the real situation in the sea. It is not unreasonable to suspect that different kinds (and sizes) of prey may sig-

---

[1] Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564.

Manuscript accepted June 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

nificantly affect the feeding and growth of fish larvae. For these reasons, there is a need for additional detailed descriptions of natural prey so that laboratory studies can be designed to investigate the effects of these prey organisms on larval fish behavior, metabolism, and growth.

This study was undertaken to examine and compare the food habits and trophic relationships of the larvae of five species of marine cottids—*Myoxocephalus aenaeus, M. octodecemspinosus, M. scorpius, Triglops murrayi,* and *Hemitripterus americanus*—during winter and early spring when they cooccur at peak abundance in the Damariscotta River estuary, Maine. Data are presented on feeding incidence, diet composition, diet overlap, larval mouth size, and prey size. Trophic patterns are examined with respect to possible interspecific competition and the influence of relative prey abundance and morphology on foraging. Aspects of the feeding ecology of these larvae are compared with the early feeding ecology of other marine fishes.

MATERIALS AND METHODS

Larvae used in diet analyses were collected in surface and bottom tows of a 1 m, 360 μm mesh conical plankton net which was mounted atop a 1.3 m wide × 45.7 cm high Blake trawl (a type of beam trawl). Although larvae were collected throughout the Damariscotta River, a drowned river valley opening into the Gulf of Maine and located on the central Maine coast, most specimens were captured in the middle basin of the estuary (Laroche 1980). *Myoxocephalus* (*M. aenaeus, M. octodecemspinosus,* and *M. scorpius*) and *T. murrayi* larvae were collected, for the most part, on these dates in 1973: 22 January; 6, 20, 21 February; and 5, 6, 19, 20 March. From 26 to 30% of larvae of the four species used in diet analyses were taken in surface tows and 70 to 74% were taken in bottom tows. Larvae of *H. americanus* were rare in collections; therefore, all specimens collected during the period January-April 1972-74 were used in diet analyses.

Prior to preservation in 10% Formalin[2] in the field, an unquantified amount of MS-222 (tricaine methanesulfonate) was added to each sample. The sample was gently swirled as the anesthetic dissolved larvae became inactive. This procedure eliminated defecation and/or regurgitation subsequent to capture.

Before removal of the gut, standard length (SL, to nearest 0.1 mm) and upper jaw length (i.e., distance from symphysis to posterior margin of maxillary along the ventral aspect, to nearest 0.01 mm) were measured using an ocular micrometer in a stereomicroscope. Jaw length rather than gape was used as a measure of potential size of the mouth opening because jaw length was not affected by whether the mouth was opened or closed at the time of preservation and could, therefore, be measured more consistently and precisely. Larvae were placed in a cavity of a double-depression glass slide, and the entire gastrointestinal tract from esophageal sphincter to anus was gently pulled intact from the abdominal cavity. At this time the presence or absence of yolk was noted, and an estimate was made of the quantity of yolk present: one-fourth, one-half, three-fourths of abdominal cavity full or only a remnant remaining. The gut was placed in the other, water-filled cavity of the slide, and the gastric and pyloric regions were teased apart separately using two fine probes. The presence or absence of food items in each of these regions was noted.

Food items were identified to the lowest taxon possible and counted except for undigestable prey remains, such as setae, and unrecognizable debris. *Pseudocalanus* eggs, which were probably ingested with the brooding females, and small diatoms (in March samples only) were likewise not counted. Maximum body width or diameter of most food items was measured.

Larvae were grouped into arbitrarily chosen size intervals, based on overall size distributions, to facilitate intra- and interspecific diet comparisons. Percent frequency of occurrence (%*FO*) and percent of total number (%*N*) of prey ingested by larvae in each size group were calculated for each food category. An estimate of the relative importance of each food category was obtained by multiplying %*FO* by %*N*. Diet overlap was measured using the Schoener index (1970):

$$\alpha = 100\ [1 - 0.5 \sum_{i=1}^{n} /p_{xi} - p_{yi}/],$$

where p_{xi} = proportion (percent by number) of food category i in the diet of species x; p_{yi} = proportion (percent by number) of food category i in the diet of species y; and n = the number of food categories. Percent by volume or weight is, in most cases, more useful than %*N* or %*FO* in measuring diet overlap. However, for predators like larval *Myoxocephalus* and *T. murrayi* whose prey are similar in size (Fig. 1), calculation of the Schoener index using %*N* and %*FO* produces a relatively unbiased estimate of diet overlap (Wallace 1981).

---

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Settled volumes of the ichthyoplankton samples were measured by displacement method in either a 100 or 250 ml graduated cylinder after large jellyfish and macrophytic algae or other large plant debris were removed.

RESULTS

Feeding Incidence

The percentage of cottid larvae with empty guts ranged from 0 to 13 depending on the species, with *T. murrayi* having the lowest overall incidence of empty guts and *H. americanus* the highest (Table 1). Only *M. aenaeus* and *M. scorpius* had equal or higher percentages of empty guts in January and February than in March. In addition to this high incidence of feeding, many larvae examined had begun to feed before yolk absorption was complete (Table 1). A remnant of yolk (often sizeable) was found attached to or closely associated with the liver in feeding larvae over a wide size range: 5.3-9.5 mm SL in *M. aenaeus*; 7.2-11.5 mm SL in *M. octodecemspinosus*; 7.5-10.4 mm SL in *M. scorpius*; 8.5-12.0 mm SL in *T. murrayi*; and 12.0-15.9 mm SL in *H. americanus*.

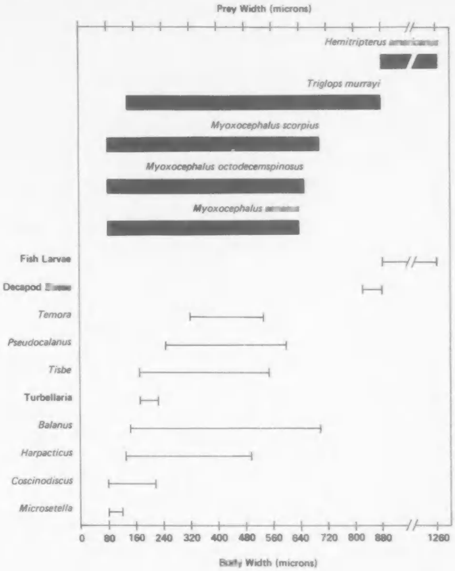


FIGURE 1.—Range in maximum body width (microns) of the major prey ingested by larvae of five species of cottids in the Damariscotta River estuary, Maine.

Among the three species of *Myoxocephalus* larvae with three-fourths of the abdominal cavity filled with yolk ($N = 33$), about 80% had food in their guts. The number of food items found in these larvae ranged from 1 to 4 in *M. aenaeus*, 2 to 12 in *M. octodecemspinosus*, and 1 to 21 in *M. scorpius*. No yolk-sac larvae of *T. murrayi* were collected. Of the seven *H. americanus* larvae with prominent yolk sacs, only two had empty guts. Each of the other larvae contained one food item.

Diet Composition

Gut contents were examined of 147 *M. aenaeus*, 5.3-9.5 mm SL; 106 *M. octodecemspinosus*, 7.2-12.4 mm SL; 87 *M. scorpius*, 7.5-13.4 mm SL; 58 *T. murrayi*, 8.5-18.1 mm SL; and 24 *H. americanus*, 12.0-16.2 mm SL (Tables 2-10). Percent number of *Coscinodiscus* sp. was calculated only

TABLE 1.—Incidence of *Myoxocephalus*, *Triglops*, and *Hemitripterus* larvae with empty guts, and those with both food and a remnant of yolk present. (*N* = number of larvae examined.)

	January-February			March		
Species	*N*	% empty	% with yolk + food	*N*	% empty	% with yolk + food
Myoxocephalus aenaeus	18	6	94	129	6	75
M. octodecemspinosus	31	0	100	75	5	66
M. scorpius	18	11	89	69	0	91
Triglops murrayi	22	0	73	36	3	6
	January-April					
Hemitripterus americanus	24	13	83			

TABLE 2.—Summary of food habits of 18 *Myoxocephalus aenaeus* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)							
	5.3-6.4				6.5-7.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	7.1	1	0.8
Calanoid copepods:								
Temora longicornis					1	7.1	3	2.5
Harpacticoid copepods:								
Microsetella norvegica	3	75.0	9	81.8	14	100.0	104	85.2
Tisbe spp.					2	14.3	2	1.6
Unidentified:								
Adults and copepodites					1	7.1	1	0.8
Coscinodiscus sp.	1	25.0	2	18.2	7	50.0	11	9.0
Total no. food items			11				122	
Number larvae examined	4				14			
Number larvae empty	1				0			

TABLE 3.—Summary of the food habits of 129 *Myoxocephalus aenaeus* larvae captured on 5, 6, 19, and 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)															
	5.5-6.4				6.5-7.4				7.5-8.4				8.5-9.5			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	12	100.0	34	61.8	43	93.5	158	57.5	37	88.1	115	42.6	20	95.2	90	54.9
Calanoid copepods:																
Temora longicornis					3	6.5	4	1.5	9	21.4	16	5.9	4	19.0	5	3.0
Harpacticoid copepods:																
Microsetella norvegica	4	33.3	9	16.4	24	52.2	47	17.1	23	54.8	51	18.9	13	61.9	12	7.3
Tisbe spp.					10	21.7	13	4.7	10	23.8	20	7.4	5	23.8	9	5.5
Harpacticus spp.					2	4.3	2	0.7	13	31.0	17	6.3	6	28.6	9	5.5
Zaus sp.					2	4.3	2	0.7	3	7.1	4	1.5				
Unidentified:																
Adults and copepodites					5	10.9	6	2.2	3	7.1	4	1.5	1	4.8	2	1.2
Unidentified copepod nauplii					1	2.2	1	0.4					1	4.8	25	15.2
Turbellaria	3	25.0	4	7.3	13	28.3	19	6.9	12	28.6	23	8.5	4	19.0	7	4.3
Ostracoda					2	4.3	2	0.7								
Unidentified invertebrate eggs:																
Single	1	8.3	7	12.7	7	15.2	21	7.6	2	4.8	13	4.8				
Sacs	1	8.3	1	1.8					6	14.3	7	2.6	4	19.0	5	3.0
Coscinodiscus sp.	3	25.0	—		10	21.7	—		10	23.8	—		7	33.3	—	
Setae	2	16.7	—		5	10.9	—		11	26.2	—		3	14.3	—	
Unrecognizable debris	5	41.7	—		13	28.3	—		20	47.6	—		12	57.1	—	
Total no. food items			55				275				270				164	
Number larvae examined	17				49				42				21			
Number larvae empty	5				3				0				0			

in January-February and not in March when barnacle nauplii were the principal prey of larvae, because it is likely that some proportion of these diatom cells were released from the guts of *Balanus* nauplii during digestion. Cells ≦25 μm in diameter were found inside undigested *Balanus* nauplii taken from the guts of cottid larvae. Flatworms (Turbellaria) ingest diatoms whole (Jennings 1957) and these may also have contributed *Coscinodiscus* cells. Most of the calanoid and harpacticoid copepods ingested by cottid larvae were adults and, for *Temora longicornis*, mostly females. Bundles of setae of undetermined origin seemed to accumulate in the guts of cottid larvae. The most likely sources of these are the appendages of *Microsetella* and *Balanus* nauplii.

Diet Comparisons

Relative importance of each prey taxon was estimated from the product of %*FO* and %*N*. Major prey (%*FO* × %*N*>100) of only similar-sized larvae were ranked according to this value and compared for seasonal as well as inter- and intraspecific differences (Tables 11, 12). In general, the same trophic patterns were present among larvae in size groups not included in these comparisons (Tables 2-10).

In January and February the dominant prey of

TABLE 4.—Summary of the food habits of 31 *Myoxocephalus octodecemspinosus* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)							
	7.2-8.4				8.5-9.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					2	28.6	2	1.7
Calanoid copepods:								
Temora longicornis	7	29.2	8	2.5	7	100.0	28	23.3
Harpacticoid copepods:								
Microsetella norvegica	24	100.0	284	89.3	7	100.0	65	54.2
Tisbe spp.	2	8.3	2	0.6				
Harpacticus spp.	2	8.3	2	0.6				
Unidentified:								
Adults and copepodites	3	12.5	3	0.9	2	28.6	3	2.5
Unidentified copepod nauplii	2	8.3	3	0.9	1	14.3	2	1.7
Ostracoda	1	4.2	1	0.3				
Unidentified invertebrate eggs:								
Single					2	28.6	20	16.7
Coscinodiscus sp.	3	12.5	15	4.7				
Setae	1	4.2	—					
Total no. food items			318				120	
Number larvae examined	24				7			
Number larvae empty	0				0			

both *M. aenaeus* and *M. octodecemspinosus* was *Microsetella norvegica*, while *Coscinodiscus* sp. dominated the diet of *Myoxocephalus scorpius* larvae. *Coscinodiscus* sp. cells are bright green in color and the digestive tracts of *M. scorpius* larvae observed in the field before preservation appeared to be this same color. Unlike similar-sized *M. octodecemspinosus* and *M. scorpius*, *Triglops murrayi* larvae fed primarily on adult *Pseudocalanus minutus* and calanoid copepodites, which were largely digested but most resembled, and probably were, immature *Pseudocalanus*. There appeared to be no distinct change in dominant prey types as larvae grew within the size ranges examined. The largest *M. octodecemspinosus* and *M. scorpius* larvae ingested more kinds of prey than smaller larvae, but the reverse was true for *T. murrayi*.

In March, the overwhelmingly dominant prey of all three species of *Myoxocephalus* were *Balanus* nauplii. *Microsetella* ranked second in importance among 7.5-9.5 (9.4) mm SL *Myoxocephalus aenaeus* and *M. octodecemspinosus* larvae, but was replaced by adult *Temora longicornis* in 9.5-12.4 mm SL *M. octodecemspinosus*. No other prey of *M. scorpius* larvae at any size approached the importance of *Balanus* nauplii which were nearly the exclusive prey of this species in March. Mean number of nauplii per *M. scorpius* larva ranged from 12 to 16 depending on larval size, whereas the range in mean number for the other two species of *Myoxocephalus* was only 3-8 nauplii/larva. As in January and February, *Pseudocalanus* dominated the diet of *T. murrayi* larvae in four of six size groups. *Balanus* nauplii ranked second in importance in four size groups, and ranked first in the largest size group. Other fish larvae, primarily *M. aenaeus*, were nearly the exclusive prey of all *H. americanus* larvae examined. Up to four prey larvae were found in the gut of a single *H. americanus* larva, and a 13 mm SL rockgunnel, *Pholis gunnellus*, larva was found coiled up inside the gut of a 13 mm SL specimen. There was no dramatic change in prey types ingested among the five species with increasing larval size. Only the change in the second-ranked prey of *M. octodecemspinosus* larvae from *Microsetella* to *Temora* may have been related to increased size.

The most important seasonal change in diet among cottid larvae was replacement of *Coscinodiscus* sp. and, to a lesser extent, *Microsetella* by *Balanus* nauplii. Barnacle nauplii also became a relatively important component of the diet of *T. murrayi* larvae in March but *Pseudocalanus* continued to dominate the diet of larvae in most size groups.

Diet Overlap

Diet overlap was measured among larvae of four species of cottids (*H. americanus* excluded because of its obviously unique diet), using the Schoener index (1970) which describes the relative amount of dietary overlap between species pairs on a scale of 0 = no overlap to 100 = com-

TABLE 5.—Summary of the food habits of 75 *Myoxocephalus octodecemspinosus* larvae captured on 5, 6, 19, 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

Food item	Size range (mm)																			
	7.5-8.4				8.5-9.4				9.5-10.4				10.5-11.4				11.5-12.4			
	FO	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	4	80.0	17	39.5	23	95.8	117	45.3	21	87.5	126	61.8	11	84.6	76	76.8	3	60.0	42	77.8
Calanoid copepods:																				
Temora longicornis	1	20.0	2	4.7	8	33.3	14	5.4	13	54.2	36	17.6	9	69.2	17	17.2	4	80.0	11	20.4
Harpacticoid copepods:																				
Microsetella norvegica	3	60.0	19	44.2	16	66.7	51	19.8	11	45.8	26	12.7	1	7.7	2	2.0				
Tisbe spp.					3	12.5	3	1.2	2	8.3	3	1.5	1	7.7	1	1.0				
Harpacticus spp.	1	20.0	2	4.7									1	7.7	1	1.0				
Unidentified:																				
Adults and copepodites	1	20.0	1	2.3	1	4.2	1	0.4	2	8.3	2	1.0	1	7.7	1	1.0				
Unidentified invertebrate eggs:																				
Single	1	20.0	1	2.3	6	25.0	69	26.7	1	4.2	9	4.4	1	7.7	1	1.0	1	20.0	1	1.9
Sacs	1	20.0	1	2.3	3	12.5	3	1.2	1	4.2	2	1.0								
Coscinodiscus sp.	2	40.0	—		2	8.3	—		3	12.5	—		2	1.5			2	40.0	—	
Setae	2	40.0	—		5	20.8	—		6	25.0	—		3	2.3	—					
Unrecognizable debris	2	40.0	—		7	29.2	—		9	37.5	—		7	5.4	—		2	40.0	—	
Total no. food items			43				258				204				99				54	
Number larvae examined	7				25				25				13				5			
Number larvae empty	2				1				1				0				0			

TABLE 6.—Summary of the food habits of 18 *Myoxocephalus scorpius* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

Food item	Size range (mm)											
	7.5-8.4				8.5-9.4				9.5-10.4			
	FO	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	11.1	2	0.9	3	100.0	3	3.1
Calanoid copepods:												
Temora longicornis					1	11.1	1	0.5	2	66.7	3	3.1
Pseudocalanus minutus					1	11.1	1	0.5				
Unidentified									1	33.3	1	1.0
Harpacticoid copepods:												
Microsetella norvegica	2	50.0	2	6.1	3	33.3	7	3.2	1	33.3	2	2.0
Tisbe spp.									1	33.3	1	1.0
Harpacticus spp.					2	22.2	2	0.9	1	33.3	1	1.0
Zaus sp.					2	22.2	3	2.8				
Unidentified:												
Adults and copepodites					3	33.3	3	1.4	3	100.0	10	10.2
Nauplii					1	11.1	27	12.5	1	33.3	30	30.6
Unidentified invertebrate eggs:												
Single					3	33.3	62	28.7	1	33.3	25	25.5
Coscinodiscus sp.	3	75.0	31	93.9	8	88.9	108	50.0	3	100.0	22	22.4
Unrecognizable debris	1	25.0	—		2	22.2	—		1	33.3	—	
Total no. food items			33				216				98	
Number larvae examined	6				9				3			
Number larvae empty	2				0				0			

TABLE 7.—Summary of food habits of 69 *Myoxocephalus scorpius* larvae captured on 5, 6, 19, 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																			
	8.5-9.4				9.5-10.4				10.5-11.4				11.5-12.4				12.5-13.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	14	100.0	165	94.3	28	96.6	426	77.3	12	100.0	182	90.1	8	100.0	120	91.6	6	100.0	95	93.1
Calanoid copepods:																				
Temora longicornis					8	27.6	12	2.2	2	16.7	8	4.0	2	25.0	4	3.1	1	16.7	1	1.0
Unidentified:																				
Adults and copepodites					5	17.2	5	0.9	1	8.3	2	1.0	2	25.0	2	1.5				
Harpacticoid copepods:																				
Tisbe spp.					9	31.0	11	2.0	3	25.0	3	1.5	2	25.0	2	1.5	3	50.0	3	2.9
Harpacticus spp.					7	24.1	9	1.6	3	25.0	3	1.5	1	12.5	1	0.8				
Zaus sp.	1	7.1	1	0.6	3	10.3	3	5.4					1	12.5	2	1.5	1	16.7	1	1.0
Unidentified:																				
Adults and copepodites	1	7.1	1	0.6	2	6.9	8	1.5	1	8.3	2	1.0					1	16.7	1	1.0
Unidentified invertebrate eggs:																				
Single	2	14.3	8	4.6	5	17.2	77	14.0	2	16.7	2	1.0								
Sacs																	1	16.7	1	1.0
Coscinodiscus sp.	2	14.3	—		5	17.2	—		3	25.0	—		3	37.5	—		1	16.7	—	
Setae					3	10.3	—		1	8.3	—		2	25.0	—		1	16.7	—	
Unrecognizable debris	5	35.7	—		10	34.5	—		5	41.7	—		4	50.0	—		2	33.3	—	
Total no. food items			175				551				202				131				102	
Number larvae examined	14				29				12				8				6			
Number larvae empty	0				0				0				0				0			

TABLE 8.—Summary of the food habits of 22 *Triglops murrayi* larvae captured on 22 January and 6, 20, 21 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																			
	8.5-8.9				9.0-10.4				10.5-11.4				11.5-12.4				12.5-14.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii																	1	33.3	1	2.2
Calanoid copepods:																				
Temora longicornis	1	20.0	2	10.0	1	20.0	1	2.9					2	50.0	8	18.6	2	66.7	7	15.6
Pseudocalanus minutus	5	100.0	9	45.0	5	100.0	20	57.1	5	100.0	17	77.3	4	100.0	31	72.1	3	100.0	24	53.3
Unidentified:																				
Adults					1	20.0	1	2.9					1	25.0	1	2.3				
Copepodites	4	80.0	8	40.0	5	100.0	13	37.0	3	40.0	5	22.7	3	75.0	3	7.0	2	66.7	12	26.7
Nauplii																	1	33.3	1	2.2
Pseudocalanus eggs					1	20.0	—		3	40.0	—		1	25.0	—					
Harpacticoid copepods:																				
Tisbe sp.	1	20.0	1	5.0																
Unrecognizable debris					2	40.0	—													
Total no. food items			20				35				22				43				45	
Number larvae examined	5				5				5				4				3			
Number larvae empty	0				0				0				0				0			

TABLE 9.—Summary of the food habits of 36 *Triglops murrayi* larvae captured on 5, 6, 19, 20 March 1973. %FO = percent frequency of occurrence (FO) among larvae containing food; %N = percent of the total number (N) of food items ingested by larvae in that size group.

	Size range (mm)																											
	9.0-10.4				10.5-11.4				11.5-12.4				12.5-13.4				13.5-14.4				14.5-15.4				15.5-18.1			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%N	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	33.3	7	43.8	2	40.0	21	33.3	2	50.0	15	45.5	4	66.7	33	42.9	5	100.0	31	62.0	9	100.0	59	64.8
Calanoid copepods:																												
Temora longicornis																	2	33.3	2	2.6	3	60.0	8	16.0	2	10.3	9	9.9
Pseudocalanus minutus	2	100.0	6	85.7	2	66.7	7	43.8	3	60.0	6	9.5	4	100.0	16	48.5	6	100.0	29	37.7	3	60.0	8	16.0	7	77.8	14	15.4
Unidentified:																												
Adults					1	33.3	1	6.3	1	20.0	1	1.6													1	11.1	4	4.4
Copepodites	1	50.0	1	14.3					1	20.0	1	1.6	2	50.0	2	6.1	2	33.3	2	2.6	1	20.0	1	2.0	1	11.1	1	1.1
Pseudocalanus eggs					2	66.7	—						1	25.0	—		2	33.3	—		1	20.0	—		3	33.3	—	
Unidentified:																												
Harpacticoid copepods									1	20.0	1	1.6																
Cyclopoid copepods					1	33.3	1	6.3																				
Decapod zoea																	1	16.7	1	1.3	1	20.0	1	2.0	4	44.4	4	4.4
Unidentified invertebrate eggs									2	40.0	33	52.4					1	16.7	10	13.0	1	20.0	1	2.0				
Unrecognizable debris									1	20.0	—						2	33.3	—		3	60.0	—		8	88.9	—	
Total no. food items			7				16				63				33				77				50				91	
Number larvae examined	4				3				5				4				6				5				9			
Number larvae empty	1				0				0				0				0				0				0			

TABLE 10.—Summary of the food habits of 24 *Hemitripterus americanus* larvae captured on 22 January 1974; 16 February 1972; 7 March 1972; 5, 6, 20 March 1973; 6 March 1974; and 12 April 1972. %FO = percent frequency of occurrence (FO) among larvae containing food; %N = percent of the total number (N) of food items ingested by larvae in that size group.

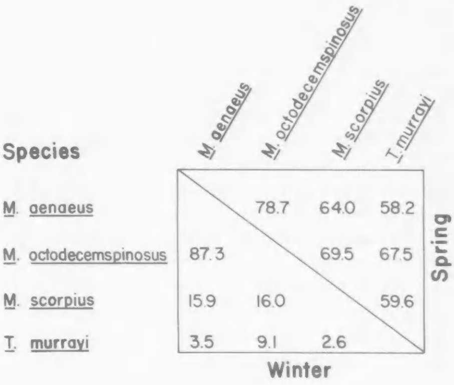
	Size range (mm)															
	12.0-13.4				13.5-14.4				14.5-15.4				15.5-16.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Decapod zoea					1	20.0	1	20.0								
Fish larvae[1]	8	100.0	9	100.0	4	80.0	4	80.0	4	100.0	6	100.0	4	100.0	8	100.0
Total no. food items			9				5				6				8	
Number larvae examined	10				6				4				4			
Number larvae empty	2				1				0				0			

[1] Includes:
1 - *Pholis gunnellus* (~13 mm SL)
1 - *Lumpenus lampretaeformis*
12 - *Myoxocephalus aenaeus* (~5-6 mm SL)
1 - *M. octodecemspinosus* (~7-8 mm SL)
1 - *Triglops murrayi*
6 - Unidentified cottid larvae
5 - Unidentified fish larvae.

TABLE 11.—Comparison of the major prey of similar-sized cottid larvae from January and February 1973. Food items are listed in order of decreasing rank by the value (in parentheses) of the product, % frequency of occurrence × % of total number; only items with a value >100 are presented. Food item abbreviations are: BN = *Balanus* nauplii; Cosc = *Coscinodiscus* sp.; $E_{(si)}$ = Invertebrate eggs (single); Mn = *Microsetella norvegica*; Ps = *Pseudocalanus minutus*; Tem = *Temora longicornis*; Ts = *Tisbe* spp.; UCalc = Unidentified calanoid copepodites; UHa or n = Unidentified harpacticoid adults or nauplii.

Myoxocephalus aenaeus			
Size range (mm)	6.5-7.4		
Ranked food items	Mn (8,500) Cosc (450)		
Myoxocephalus octodecemspinosus			
Size range (mm)	7.2-8.4	8.5-9.4	
Ranked food items	Mn (8,900)	Mn (5,420) Tem (2,330) $E_{(si)}$ (478)	
Myoxocephalus scorpius			
Size range (mm)	7.5-8.4	8.5-9.4	9.5-10.4
Ranked food items	Cosc (7,043) Mn (305)	Cosc (4,445) $E_{(si)}$ (956) UHn (139) Mn (106)	Cosc (2,240) UHn (1,029) UHa (1,000) $E_{(si)}$ (849) BN (300) Tem (200)
Triglops murrayi			
Size range (mm)		8.5-8.9	9.0-10.4
Ranked food items		Ps (4,500) UCalc (3,200) Tem (200) Ts (100)	Ps (5,700) UCalc (3,700)

plete overlap (Fig. 2). Except for the consistently high degree of overlap between the diets of *Myoxocephalus aenaeus* and *M. octodecemspinosus*, overlap among cottid larvae in general


Spring
Winter

Species	M. aenaeus	M. octodecemspinosus	M. scorpius	T. murrayi
M. aenaeus		78.7	64.0	58.2
M. octodecemspinosus	87.3		69.5	67.5
M. scorpius	15.9	16.0		59.6
T. murrayi	3.5	9.1	2.6	

FIGURE 2.—Matrix of Schoener (1970) index values measuring percent diet overlap among species pairs of cottid larvae from winter (January-February) and early spring (March) collections in the Damariscotta River estuary, Maine.

TABLE 12.—Comparison of the major prey of similar-sized cottid larvae from March 1973 (*Myoxocephalus* spp. and *T. murrayi*) and January-April 1972-74 (*H. americanus*). Food items are listed in order of decreasing rank by the value (in parentheses) of the product, % frequency of occurrence × % of total number; only items with a value >100 are presented. Food item abbreviations are: BN = *Balanus* nauplii; DZ = decapod zoea; $E_{(si)}$ = Invertebrate eggs (single); FL = fish larvae; H = *Harpacticus* spp.; Mn = *Microsetella norvegica*; Ps = *Pseudocalanus minutus*; Tem = *Temora longicornis*; Ts = *Tisbe* spp.; Tur = Turbellaria; UCala or c = Unidentified calanoid adults or copepodites; UCyc = Unidentified cyclopoids. (* = tied rank.)

Myoxocephalus aenaeus								
Size range (mm)	7.5-8.4	8.5-9.5						
Ranked food items	BN (3,753) Mn (1,036) Tur (243) H (195) Ts (176) Tem (126)	BN (5,226) Mn (452) H (157) Ts (131)						
Myoxocephalus octodecemspinosus								
Size range (mm)	7.5-8.4	8.5-9.4	9.5-10.4	10.5-11.4	11.5-12.4			
Ranked food items	BN (3,160) Mn (2,652)	BN (4,340) Mn (1,321) $E_{(si)}$ (668) Tem (180)	BN (5,408) Tem (954) Mn (582)	BN (6,497) Tem (1,190)	BN (4,668) Tem (1,632)			
Myoxocephalus scorpius								
Size range (mm)		8.5-9.4	9.5-10.4	10.5-11.4	11.5-12.4	12.5-13.4		
Ranked food items		BN (9,430)	BN (7,467) $E_{(si)}$ (241)	BN (9,000)	BN (9,160)	BN (9,310) Ts (145)		
Triglops murrayi								
Size range (mm)			9.0-10.4	10.5-11.4	11.5-12.4	12.5-13.4	13.5-14.4	14.5-15.4
Ranked food items			Ps (8,570) UCalc (715)	Ps (2,921) BN (1,459) *UCala (210) *UCyc (210)	$E_{(si)}$ (2,096) BN (1,459) Ps (570)	Ps (4,850) BN (1,332) UCalc (305)	Ps (3,770) BN (2,275) $E_{(si)}$ (217)	BN (6,200) *Ps (960) *Tem (960)
Hemitripterus americanus								
Size range (mm)						12.0-13.4	13.5-14.4	14.5-15.4
Ranked food items						FL (10,000)	FL (6,400) DZ (400)	FL (10,000)

was greater in early spring (March) than in winter (January and February). Diets of the three species of *Myoxocephalus* usually overlapped more with each other than did any with the diet of *T. murrayi*. This difference was more pronounced in winter than in early spring.

Larval Mouth Size and Prey Width

Because mouth size or gape determines maximum size of prey ingested, the ratio of upper jaw length (mm) to standard length (mm) was used to compare relative mouth sizes among cottid larvae (Blaxter and Hempel 1963; Shirota 1970). Jaw length to standard length ratios were most similar at all stages of development among the three species of *Myoxocephalus* (Table 13). Larvae of *T. murrayi* and *H. americanus*, regardless of stage of development, had larger mouths than *Myoxocephalus* larvae. Only *H. americanus* larvae had jaw teeth within the size range observed.

All food items found in cottid larvae had been swallowed whole. Since fish larvae have been observed to swallow their prey head-first with appendages and setae folded back, the critical dimension of a potential food item is maximum body width (Blaxter 1965; Arthur 1976). Maximum widths of the major prey of larval cottids ranged from 80 to 1,260 μm (Fig. 1). Among individual prey items, *Balanus* nauplii exhibited the widest size range and *Microsetella* the narrowest. The harpacticoid and calanoid copepods were somewhat similar in size, while the largest prey overall were decapod zoea and fish larvae.

Prey size at first feeding was estimated for larvae of *Myoxocephalus* and *H. americanus* from the width of prey found in guts of larvae with three-fourths or more of their abdomens full of yolk. No yolk-bearing larvae of *T. murrayi* were found with this condition. *Myoxocephalus aenaeus* ($N = 14$) ingested *Microsetella* and stage 2 or 3 *Balanus* nauplii ranging in size from 100 to 360 μm. *Myoxocephalus octodecemspinosus* ($N = 5$) ingested only 100 μm wide *Microsetella*. *Myoxocephalus scorpius* ($N = 9$) ingested primarily *Coscinodiscus* and *Microsetella* which ranged from 80 to 220 μm; however, a single *Balanus* nauplius and unidentified harpacticoid copepod were found measuring 375 and 260 μm, respectively. First-feeding *H. americanus* larvae were also primarily piscivorous. Maximum width of most prey larvae (dorsally across the eyes) could not be measured because of advanced state of digestion, but one intact larva measured 950 μm. The only other prey found in yolk-sac *H. americanus* larvae was an 880 μm wide decapod zoea.

No consistent pattern of increased prey size with increased larval size or advanced stage of development was apparent over the size range of cottid larvae observed in these analyses. Overall size range of prey ingested by *Myoxocephalus* and *T. murrayi* larvae overlapped extensively (Fig. 1). Among *Myoxocephalus* larvae, *M. scorpius* ingested slightly larger prey than did the other two species which reflects the greater frequency of *Balanus* nauplii and low incidence of *Microsetella* in its diet. *Triglops murrayi* larvae ate food items over the widest size range and *H. americanus* over the narrowest size range.

DISCUSSION

The incidence of yolk retention in feeding cottid larvae was high over a wide size range, presumably representing a long period of time. Initiation of feeding before complete yolk absorption has been previously observed among larval flatfishes, gadoids, and herring (Blaxter 1965; Last 1978a, b; Sumida and Moser 1980). Arthur (1976), however, never found both yolk and ingested food in larvae of northern anchovy, *Engraulis mordax*; Pacific sardine, *Sardinops sagax*; or jack mackerel, *Trachurus symmetricus*. Food ingestion prior to complete yolk absorption may be advantageous to fish larvae by allowing time for trial-and-error learning, which has been

TABLE 13.—Comparison of relative mouth size among larval cottids using the ratio of upper jaw length (mm) to standard length (SL). N = number of larvae measured.

	Larvae used in diet analysis				Smallest larvae with yolk sac			
			Upper jaw length/SL				Upper jaw length/SL	
Species	*N*	Mean SL (mm)	Mean	Range	*N*	Mean SL (mm)	Mean	Range
Myoxocephalus aenaeus	84	7.4	0.11	0.10-0.13	12	6.3	0.10	0.09-0.10
M. octodecemspinosus	72	9.7	0.11	0.09-0.13	15	7.7	0.10	0.09-0.11
M. scorpius	61	10.3	0.12	0.09-0.13	10	8.4	0.11	0.09-0.12
Triglops murrayi	35	13.8	0.13	0.12-0.15	1	7.1	(0.13)	—
Hemitripterus americanus	20	13.9	0.15	0.13-0.17	1	13.0	(0.15)	—

shown to increase feeding success in early larvae (Blaxter 1965; Hunter 1980), as well as by prolonging the time before larvae become totally dependent on an exogenous food supply which is limited in abundance and distribution (Laurence and Rogers 1976). Potential or actual energy deficits prior to or coincident with the initiation of feeding were found to occur in the tautog, *Tautoga onitis* (Laurence 1973), and Pacific sardine, *Sardinops sagax* (Lasker 1962), both relatively fecund species having planktonic eggs and larvae. Yet, deficits based on the amount of yolk absorbed did not occur until after feeding had begun in rainbow trout, *Salmo gairdneri*; brown trout, *Salmo trutta*; bluegill, *Lepomis macrochirus*; and largemouth bass, *Micropterus salmoides*, all of which have relatively low fecundity, and demersal eggs and larvae (Laurence 1973). Although energy budgets have not been described for them, it is likely that cottids have yolk-utilization characteristics similar to this latter group of fishes.

The relatively higher incidence of empty guts among the almost exclusively piscivorous larvae of *H. americanus* may also be related to trophic energetics. Since fish larvae probably supply more energy per unit effort as prey than do crustaceans because of larger size and lack of indigestible exoskeletons, ingestion of single, large, highly digestible prey would reduce the need for continuous foraging. Larvae of *H. villosus* in the Japan Sea, like those of its congener in the Gulf of Maine, also feed on other fish larvae (Okiyama and Sando 1976). Most reports of piscivorous larvae have come from observations of laboratory-reared larvae, particularly scombroid fishes (Beyer 1980; Hunter 1980).

The larval diets of four of five species of cottids in the Damariscotta River estuary were distinctly different, despite similarities in mouth size and morphology and the absence of obvious specialized morphological adaptations for feeding. Last (1978a) also observed differences in larval diets among pleuronectiform fishes in the North Sea and concluded that this represented a mechanism whereby direct competition for food is avoided. There are many theoretical and practical difficulties in assessing the significance of competition as a cause of dietary divergence in fishes (Zaret and Rand 1971; Weatherly 1972), yet existence of competition among tropical stream fishes has been inferred from observed reductions in diet overlap during periods of lowered food supply (Zaret and Rand 1971). Comparisons of dietary overlap and food supply among the larvae of *Myoxocephalus* and *Triglops* species during winter and early spring indicated a similar pattern. The lowest values of percent diet overlap, i.e., occurrence of the most dissimilar diets, among five of six possible pairs of species combinations occurred in January and February, and coincided with lowest prey abundance as indicated by the lower mean plankton volume (an approximate measure of food supply) of the two periods compared, 16.8 ml ($n = 22$) vs. 31.0 ml ($n = 25$) in March.

Percentage diet overlap between *M. aenaeus* and *M. octodecemspinosus*, whose larvae were the most abundant in the estuary (Laroche 1980) and who had the most similar food habits, remained relatively high and constant through winter and early spring. Some mechanism other than dietary shifts, i.e., changes in dominant prey, may act to reduce competition between larvae of these two species. Although both species were more abundant 1.5 m above the bottom than in the upper 1.5 m during winter and spring months, *M. aenaeus* larvae were 5 times more abundant while *M. octodecemspinosus* were only 1.7 times more abundant (Laroche 1980). Such relative differences in vertical distribution resulted in spatial separation of most *M. aenaeus* and *M. octodecemspinosus* larvae. If competition is indeed an important factor in diet determination among cottid larvae, this spatial separation may explain the high degree of dietary overlap between these two species.

Density-independent food exploitation (Hyatt 1979) by fish larvae has not been demonstrated by quantitative comparisons of prey abundance in larval guts to their abundance in the plankton. Blaxter (1965) cited numerous examples, mostly qualitative, of apparent selection among herring larvae for specific taxa of copepod and diatom prey over other prey which were more abundant in the plankton. Qualitative comparisons of the composition and relative abundance of the zooplankton present during winter and spring months of 1972 in the Damariscotta River estuary (Lee 1974) and prey found in larval cottids from winter and spring 1973 yielded indirect evidence of density-independent foraging among these larvae. Although zooplankton species composition and abundance may vary from year to year, relative constancy has been demonstrated in larval diets of at least two of the five species of cottids in the estuary. Townsend (1981) observed that the principal prey of *M. octodecemspinosus*

(*Microsetella*, *Temora*, and *Balanus* nauplii) and *M. scorpius* larvae (*Balanus* nauplii and *Coscinodiscus*) in the Damariscotta River estuary during winter and spring 1979 were the same as reported from 1973.

Copepods which were relatively abundant during winter and spring months in the Damariscotta River estuary were *Eurytemora herdmani*, *Oithona similis*, and *Pseudocalanus minutus* (Lee 1974). Of these species only *Pseudocalanus* was an important prey of cottid larvae (one species, *Triglops*). *Oithona*, a relatively small cyclopoid, was abundant in early spring but was not eaten by cottid larvae. However, two somewhat larger species were eaten: *Temora longicornis*, whose abundance in winter was variable and lower than in summer and fall, and *Pseudocalanus*. Ivlev (1961) noted that when food is plentiful, fish will take the largest available prey present. But this does not explain why larvae preferentially ate *Temora* and not the same-sized but probably more abundant *Eurytemora* or why they apparently "preferred" the smaller species of pelagic, harpacticoid copepod, *Microsetella norvegica*, over the larger, abundant winter species *Parathalestris croni*. It is perhaps significant that four of the five major prey of *Myoxocephalus* and *Triglops* larvae, *Balanus* nauplii, *Temora*, *Pseudocalanus*, and *Microsetella* were also found to be important natural prey of fish larvae in widely different regions (Lebour 1918, 1919; Sherman and Honey 1971; Arthur 1976; Last 1978a, b). Food selection by fish larvae is controlled by factors such as prey size (the most investigated variable), morphology, catchability (as determined by swimming speeds, escape responses, etc.), and availability (temporal and spatial distribution). None of these factors are well understood.

Most studies of the feeding ecology of fish larvae have focused on prey size, but color (Arthur 1976) and body transparency may also be important cues for "selection" of various copepod prey by fish larvae. All of the harpacticoid copepods ingested by cottid larvae were brightly colored: *Tisbe* spp., red and white stripes; *Zaus* sp., blue-green; *Harpacticus* sp., brown; and *Microsetella*, red. Furthermore, except for *Microsetella*, all are epibenthic forms whose abundance in the water column would not be expected to be high (Noodt 1971). Among the calanoid copepods, differences in body transparency and resulting visibility to predators may explain why *Temora* (which has a dense, thick carapace) was ingested by cottid larvae rather than the more abundant but nearly transparent *Oithona*.

Balanus nauplii, which at times during late winter and early spring can be the most abundant zooplankter in the Damariscotta River estuary (Lee 1974), were the most ubiquitous prey of cottid larvae and appeared to be ingested in direct relation to their abundance in the plankton, i.e., in density-dependent fashion. Comparison of frequencies of occurrence of the six naupliar stages of *Balanus* ingested by *Myoxocephalus* and *Triglops murrayi* larvae in early and late March showed that, with one exception, larvae of all four species caught in early March were feeding solely on naupliar stages 1-3 (Table 14). Later in the month when *Balanus* nauplii became the dominant zooplankter in most ichthyoplankton samples, larvae of all four species (i.e., larvae of varying size and, presumably, prey-catching ability and "preference") were feeding on all six naupliar stages. Percent frequency of occurrence of each stage was remarkably similar among the four cottid species, suggesting that these values might actually reflect relative abundance of each stage in the plankton assuming that each stage is equally susceptible to capture and ingestion. The apparent reliance of cottid larvae on *Balanus* nauplii may be explained by the tendency, observed among adult fishes, to ingest more intermediate-sized rather than larger prey when both are present in abundance (Ivlev 1961; Hyatt 1980). Among larval cottid prey, naupliar

TABLE 14.—Percent frequency of occurrence (%*FO*) of six naupliar stages of *Balanus* spp. (Crisp 1962) in the guts of four species of cottids on (1) 5-6 March and (2) 19-20 March 1973.

Species:	*M. aenaeus*		*M. octodecemspinosus*		*M. scorpius*		*T. murrayi*	
Dates: No. larvae:	(1) 40 %*FO*	(2) 78 %*FO*	(1) 35 %*FO*	(2) 40 %*FO*	(1) 33 %*FO*	(2) 37 %*FO*	(1) 13 %*FO*	(2) 23 %*FO*
Balanus nauplii								
Stage 1	7	5	12	6	6	1	—	3
Stages 2,3	93	52	87	41	91	45	100	45
Stages 4,5	—	31	—	38	0.6	41	—	48
Stage 6	—	5	—	3	—	6	—	2
Stage unknown	0.6	6	2	11	2	7	—	2

stages of *Balanus*, particularly stages 2-4, are somewhat smaller than adult *Temora* and *Pseudocalanus*.

Among fish larvae whose food habits have been reported, cottid larvae most resemble hake (genus *Merluccius*) in prey size at first feeding and in changes of prey size with growth. The first prey ingested by most marine fish larvae range in width from 50 to 100 μm (Houde 1973; Hunter 1980). First prey of hake and cottid larvae are larger: 50-400 μm for *Merluccius productus*; 500 μm mean prey width for *M. merluccius hubbsi*; 100-375 μm for three species of *Myoxocephalus*; and >800 μm for *H. americanus* (Sumida and Moser 1980; de Ciechomski and Weiss 1974). Among fish larvae that ingest 50-100 μm wide prey at first feeding, there is usually a distinct and often dramatic increase in prey size with development. This is seen typically as a change from a diet of copepod eggs and nauplii to one of advanced copepodites and adults. No dramatic increase in prey size or progression in prey types occurs in cottid and hake larvae.

Hunter (1980) recently attempted to categorize marine fish larvae into distinct ecological roles based on those behavioral and physiological traits primarily associated with feeding. Two distinct groups, engrauliform and scombriform, based on extensive field and laboratory observations of northern anchovy and Pacific mackerel larvae, emerged from his analyses. Cottid larvae share some scombriform traits such as relatively large mouths and prey. Similarities in feeding posture, maneuverability, and swimming speed may be inferred because of features in body shape shared by cottid and Pacific mackerel larvae. These larvae, however, would be expected to differ significantly in rates of metabolism and growth because of the different environmental temperature regimes they inhabit: 14°-21°C for highest abundances of Pacific mackerel (Kramer 1960) and 0°-4°C for cottid larvae (Laroche 1980). In this regard, cottid larvae more closely resemble hake larvae which inhabit deeper, colder oceanic waters than either anchovy or Pacific mackerel. Hunter (1980) suggested that hake larvae may belong to a third trophic group characterized by reliance on large prey, a feature already shown to be shared with cottid larvae, and slow metabolism and growth. Although growth rates have not been estimated for cottid larvae, increases in monthly median lengths of ≦1 mm (Laroche 1980) and relatively stationary modes in length-frequency distributions during winter and spring in the Damariscotta River estuary (Townsend 1981) may be explained, in part, by slow growth rates.

Despite some apparent similarities, there are notable differences in the early life histories of hake and the five species of cottids: for example, egg size, 0.98 vs. 1.5-4 mm; size at hatching, 2.4 vs. 5-12 mm; and stage of eye and mouth development at hatching, partial vs. complete. The significance of differences such as these in further distinguishing ecological roles among fish larvae will be better understood only after the early feeding ecology of more species has been investigated.

ACKNOWLEDGMENTS

The following individuals are gratefully acknowledged for their significant contributions to this study. Wayne A. Laroche and Paul C. Jensen guided and assisted me in the field; John Konecki, Gilbert Jaeger, Paul Montagua, and William T. Peterson patiently taught me the taxonomy of invertebrate taxa; Joseph J. Graham generously supplied sampling gear and laboratory equipment, and the numerous discussions on larval fish ecology and taxonomy with him and Stanley R. Chenoweth were invaluable; Hugh H. DeWitt and Bernard J. McAlice provided long-term support and counsel; Wayne A. Laroche, Percy L. Donaghay, and William T. Peterson read the manuscript and suggested useful ways to improve it.

LITERATURE CITED

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517-530.

BEYER, J. E.
1980. Feeding success of clupeoid fish larvae and stochastic thinking. Dana 1:65-91.

BLAXTER, J. H. S.
1965. The feeding of herring larvae and their ecology in relation to feeding. Calif. Coop. Oceanic Fish. Invest. Rep. 10:79-88.

BLAXTER, J. H. S., AND G. HEMPEL.
1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Cons. Int. Explor. Mer 28:211-240.

CRISP, D. J.
1962. The planktonic stages of the cirripedia *Balanus balanoides* (L.) and *Balanus balanus* (L.) from north temperate waters. Crustaceana 3:207-221.

DE CIECHOMSKI, J. D., AND G. WEISS.
1974. Estudios sobre la alimentacion de larvas de la mer-

luzza, *Merluccius merluccius hubbsi* y de la anchoita, *Engraulis anchoita* en el mar. Physis. Rev. Asoc. Argent. Cienc. Nat. 33:199-208.

Houde, E. D.

1973. Some recent advances and unsolved problems in the culture of marine fish larvae. Proc. World Maricult. Soc. 3:83-112.

Hunter, J. R. (editor).

1976. Report of a colloquium on larval fish mortality studies and their relation to fishery research, January 1975. U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC 395, 5 p.

Hunter, J. R.

1980. The feeding behavior and ecology of marine fish larvae. *In* J. E. Bardach, J. J. Magnuson, R. C. May, and J. M. Reinhart (editors), Fish behavior and its use in the capture and culture of fishes, p. 287-330. ICLARM (International Center for Living Aquatic Resources Management) Conference Proceedings 5, 512 p.

Hyatt, K. D.

1979. Feeding strategy. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. VIII, p. 71-119. Acad. Press, N.Y.

Ivlev, V. S.

1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, 302 p.

Jennings, J. B.

1957. Studies on feeding, digestion, and food storage in free-living flatworms (Platyhelminthes: Turbellaria). Biol. Bull. (Woods Hole) 112:63-80.

Kramer, D.

1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae 1952-1956. U.S. Fish Wildl. Serv., Fish. Bull. 60:393-438.

Laroche, J. L.

1980. Larval and juvenile abundance, distribution, and larval food habits of the larvae of five species of sculpins (Family: Cottidae) in the Damariscotta River estuary, Maine. Ph.D. Thesis, Univ. Maine, Orono, 175 p.

Lasker, R.

1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine, *Sardinops caerulea* (Girard). J. Fish. Res. Board Can. 19:867-875.

Last, J. M.

1978a. The food of four species of pleuronectiform larvae in the eastern English Channel and southern North Sea. Mar. Biol. (Berl.) 45:359-368.

1978b. The food of three species of gadoid larvae in the eastern English Channel and southern North Sea. Mar. Biol. (Berl.) 48:377-386.

Laurence, G. C.

1973. Influence of temperature on energy utilization of embryonic and prolarval tautog, *Tautoga onitis*. J. Fish. Res. Board Can. 30:435-442.

Laurence, G. C., and C. A. Rogers.

1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* (L.)). J. Cons. Cons. Int. Explor. Mer 36:220-228.

Lebour, M. V.

1918. The food of post-larval fish. J. Mar. Biol. Assoc. U.K. 11:434-469.

1919. The food of young fish No. III. J. Mar. Biol. Assoc. U.K. 12:261-324.

Lee, W.-Y.

1974. Succession and some aspects of population dynamics of copepods in the Damariscotta River estuary, Maine. Ph.D. Thesis, Univ. Maine, Orono, 184 p.

Noodt, W.

1971. Ecology of the Copepoda. *In* N. C. Hulings (editor), Proceedings of First International Conference on Meiofauna, p. 97-102. Smithson. Contrib. Zool. No. 76.

Okiyama, M., and H. Sando.

1976. Early life history of the sea raven, *Hemitripterus villosus*, (Hemitripterinae, Cottidae) in the Japan Sea. [In Jpn., Engl. abstr.] Bull. Jpn. Sea Reg. Fish. Res. Lab. 27:1-10.

Schoener, T. W.

1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408-418.

Sherman, K., and K. A. Honey.

1971. Seasonal variations in the food of larval herring in coastal waters of central Maine. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 160:121-124.

Shirota, A.

1970. Studies on the mouth size of fish larvae. [In Jpn., Engl. abstr.] Bull. Jpn. Soc. Sci. Fish. 36:353-368.

Sumida, B. Y., and H. G. Moser.

1980. Food and feeding of Pacific hake larvae, *Merluccius productus*, off southern California and northern Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 21:161-166.

Townsend, D. W.

1981. Comparative ecology and population dynamics of larval fishes and zooplankton in two hydrographically different areas on the Maine coast. Ph.D. Thesis, Univ. Maine, Orono, 282 p.

Wallace, R. K., Jr.

1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110:72-76.

Weatherly, A. H.

1972. Growth and ecology of fish populations. Acad. Press, N.Y., 293 p.

Zaret, T. M., and A. S. Rand.

1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336-342.

FOOD HABITS OF JUVENILE SALMON IN THE OREGON COASTAL ZONE, JUNE 1979

WILLIAM T. PETERSON,[1] RICHARD D. BRODEUR,[2] AND WILLIAM G. PEARCY[2]

ABSTRACT

Euphausiids, hyperiid amphipods, crab larvae, and fishes were the important prey identified from stomachs of 408 juvenile salmon collected in a purse seine along the Oregon coast in June 1979. Food habits of juvenile salmon differed among species. About 95% of the weight and numbers of prey of chum salmon consisted of euphausiids and hyperiids. Euphausiids and hyperiids were numerically the most abundant prey items of juvenile coho and chinook salmon, but, on a weight basis, over half the stomach contents consisted of fishes.

Variability in food habits was high for both juvenile coho and chinook salmon. Fishes from only 2 of 45 station pairs (coho) and 3 of 28 (chinook) had diet similarities >75%. The statistical relationship between weight of euphausiids and weight of fishes in stomachs for coho and chinook juveniles showed a strong tendency for both species to contain large amounts of either fishes or euphausiids, but not both simultaneously.

Diet overlap between coho and chinook juveniles was high overall, but low between the same 20 mm size classes of these same species. Euphausiids were eaten in equal numbers throughout the 100-200 mm coho size range; euphausiids were not eaten by chinook <180 mm fork length. Hyperiids were mainly eaten by 180-220 mm coho and by 140-180 mm chinook. Fishes were consumed mainly by juveniles of both species >160 mm.

Based on estimated zooplankton standing stocks, an average (160 mm) coho salmon would have to search and consume all prey in a minimum volume of about 2-8 m^3 per day to fill its stomach. The average abundance of juvenile coho, as determined from purse seining, was 1 smolt per 11,500 m^3, or about 1,440-5,760 times the minimum search volume. These data are related to the question of whether food limitation exists for juvenile salmonids in the sea.

Our knowledge of the ecology of salmon in the ocean, especially during early juvenile life, is scant compared with our understanding of the freshwater phase of salmon life. The first few months that juvenile salmon spend at sea have been identified as a critical period when year-class success may be affected (Gunsolus 1978[3]; Walters et al. 1978; Healey 1980). Basic studies of abundance and distribution, growth, mortality, and feeding habits of young salmon during their first few months at sea are needed to evaluate how the ocean environment and the density of juvenile salmon affect the production of adult salmon.

This paper contributes new information on feeding habits of juveniles of three species of salmon off the Oregon coast: coho, *Oncorhynchus kisutch*; chinook, *O. tshawytscha*; and chum, *O. keta*, salmon. The authors describe the food habits of each species, variability in food habits among fishes collected at different stations, diet overlap between coho and chinook, and speculate on the impact of foraging juvenile coho on zooplankton populations in coastal waters.

METHODS

Fish were collected in a purse seine 457 m long × 30 m deep, constructed of 32 mm stretch mesh with 30 meshes of 127 mm mesh along the bottom of the net. The maximum volume of water encompassed by a round haul set that fished to 10 m depth was calculated to be no more than $1.5 \times 10^5 m^3$. A total of 56 purse seine sets were made between 18 and 29 June 1979 in three regions of the Oregon coastal zone: Off the Columbia River (northern Oregon), off Newport (central Oregon), and in the vicinity of Coos Bay (southern Oregon) (Fig. 1). A total of 509 salmonids <35 cm FL (fork length) (henceforth called juveniles)

---

[1] School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Marine Sciences Research Center, State University of New York-Stony Brook, Stony Brook, NY 11794.

[2] School of Oceanography, Oregon State University, Corvallis, OR 97331.

[3] Gunsolus, R. T. 1978. The status of Oregon coho and recommendations for managing the production, harvest, and escapement of wild and hatchery-reared stocks. Intern. rep., 59 p. Oregon Department of Fish and Wildlife, Clackamas Laboratory, 17330 S.E. Evelyn Street, Clackamas, OR 97015.

Manuscript accepted April 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

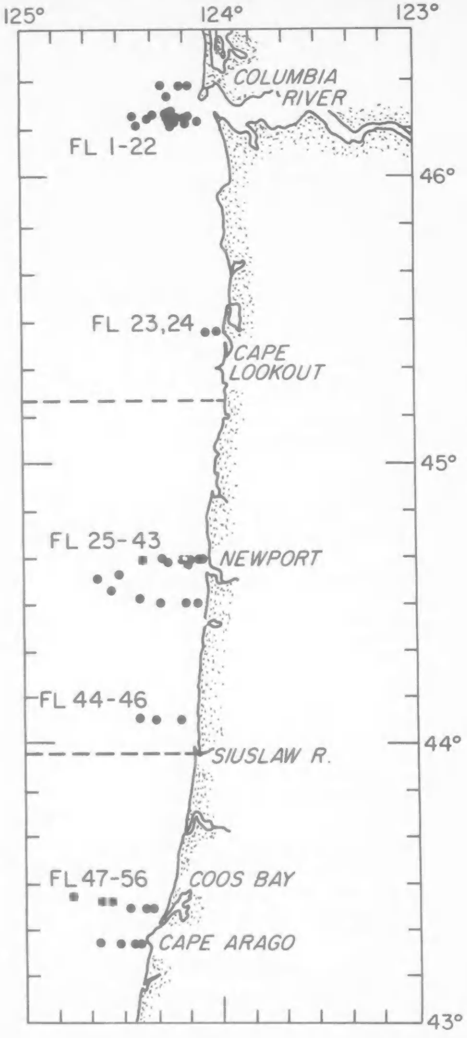


FIGURE 1.—Location of the 56 purse seine sets made by the FV *Flamingo* (FL), 18-29 June 1979. Three geographical regions were arbitrarily defined as northern (FL 1-24), central (FL 25-46), and southern (FL 47-56).

were collected in the sets. Stomach contents of 220 juvenile coho, 147 juvenile chinook, and 41 juvenile chum salmon were examined.

Whole fish <35 cm FL were preserved at sea, after slitting the body cavity, in a 5-15% Formalin[4]-seawater mixture. In the laboratory, all juvenile salmonids were identified to species, measured (fork length), and stomachs removed. Relative stomach fullness was visually estimated on a scale of 0-3 (where 0 = empty; 1, 2, and 3 = fullness in thirds; distended stomachs = 3). State of digestion was noted as one of three subjective categories: Well-digested, partially digested, or fresh. Due to the possibility of differential digestion times of prey items, categorization of state of digestion probably has little meaning except for the "fresh" category.

Food items were identified to the lowest possible taxonomic level and enumerated. Crustaceans and fishes were also identified to developmental stage. Standard length of all fish prey was measured as well as total length of most of the invertebrate taxa from the coho salmon stomachs. Euphausiid lengths were measured from the posterior edge of the eye socket to the tip of the telson. Stomach contents of all salmonids were sorted into major taxonomic groups, damp-dried on absorbent paper, and weighed to the nearest 0.01 g.

RESULTS

Occurrence and Abundances of Prey Taxa

Table 1 lists the average abundances of major taxa of prey in salmonid stomachs and the average length and length ranges of fishes examined. Euphausiids, amphipods, and crab larvae were the most numerous taxa in the stomachs of juveniles of all three species. Fishes were the only other major taxa found in all juvenile salmon. Numbers of fish per stomach were low. On a weight basis, fishes were the most important prey for juvenile coho and chinook, followed by euphausiids (Table 2). Chum stomachs contained mostly euphausiids and amphipods.

Based on percent frequency of occurrence of prey in stomachs, euphausiids occurred in 85% of all chum stomachs, 63% of coho stomachs, and about 50% of chinook and steelhead stomachs (Table 2). Amphipods also ranged in frequency of occurrence from 56 to 32% among these same species. The occurrence of fishes, on the other hand, ranged from 10% of the chum stomachs to 69 and 71% in coho and chinook stomachs, respectively.

---

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Average number of prey in individual stomachs of juvenile chum, coho, and chinook salmon. A more detailed taxonomic breakdown is given in Table 3.

Prey category	Chum	Coho	Chinook
Euphausiids	44.4	36.9	71.9
Amphipods	30.8	28.0	22.9
Fishes	1.2	4.0	4.2
Crab larvae	2.0	13.5	9.9
Copepods	1.6	6.5	3.2
Molluscs	—	10.6	1.7
Barnacle cyprids	—	4.5	—
Shrimp larvae	—	3.0	1.3
Number of stomachs	41	220	146
Number of empty stomachs	5	22	14
Average length of salmonid (mm)	124	164	208
Range in length (mm)	102-144	94-134	89-308

TABLE 2.—Average wet weight (in grams) of major prey groups found in juvenile chum, coho, and chinook salmon stomachs. Numbers in parentheses are percentages of salmon stomachs containing the specific prey item. Average weight of stomach contents is for fish with food in their stomachs. Weights of salmon are wet weights calculated from mean lengths using the length-weight equations of Healey (1980).

	Chum		Coho		Chinook	
Prey category	Wt.	%	Wt.	%	Wt.	%
Euphausiids	0.22	(85)	0.35	(63)	0.63	(51)
Amphipods	0.04	(56)	0.20	(43)	0.12	(31)
Fishes	0.07	(10)	0.73	(69)	1.04	(71)
All others	0.04	(7)	0.12	(88)	0.46	(70)
Average weight of stomach contents (g)	0.28		0.93		1.30	
Average weight of salmon (g)	23.5		55.3		140.7	
Stomach contents as % body weight	1.2		1.7		0.9	

Total weight of stomach contents of each of the three species of juvenile salmon reflects the size of the fishes sampled (Table 2). Weights of stomach contents expressed as percent of total body weight are similar, however, averaging about 1.3%.

Frequencies of occurrence and average abundances of specific prey taxa for each of the three juvenile salmon are shown in Table 3 and are referred to in the following discussion of the diets for each of the species.

Chum Salmon

The diet of chum salmon consisted mainly of the euphausiid *Thysanoëssa spinifera* and the hyperiid amphipod *Hyperoche medusarum*. Mean numerical abundances of *T. spinifera* per chum stomach collected from northern, central, and southern Oregon were 30.1, 149.7, and 3.7, respectively; abundances of hyperiids were 2.9, 104.8, and 17.5, respectively. Both these prey were most common in chum salmon stomachs collected off central Oregon, but sample sizes were so small that it is difficult to attach any real significance to these differences.

Coho Salmon

A total of 19 invertebrate and 13 fish taxa were identified from coho stomachs (Table 3). Major prey items were juvenile euphausiids (*T. spinifera*, average length about 9.0 mm), unidentified hyperiid amphipods (average length about 4.5 mm), and various fishes (most between 25 and 30 mm long). The most frequently occurring fish identified from the juvenile coho stomachs were Pacific sand lance, *Ammodytes hexapterus*; juvenile rockfishes, *Sebastes* spp.; and larval or juvenile stages of several species of flatfishes, clupeids, and osmerids.

Average length of the prey euphausiid, *T. spinifera*, was directly related to length of the juvenile coho predator. The slope of the regression line (Fig. 2) was significantly different from zero (r = 0.46, 28 df, $P{\sim}0.01$), indicating that coho between 100 and 210 mm long eat progressively larger euphausiids. Juvenile coho fed on a broad spectrum of fish prey sizes, but, again, larger fish often consumed larger prey. Coho 141-180 mm long fed mainly on fish that were 11-30 mm long, whereas 181-200 mm coho consumed mostly larger fishes, ranging from 21 to 40 mm long (Table 4). However, the regression of lengths of whole prey fishes on lengths of juvenile coho, 94-220 mm, was not significantly different from zero.

Relationships between size of coho and numbers and sizes of prey were studied for 87 juve-

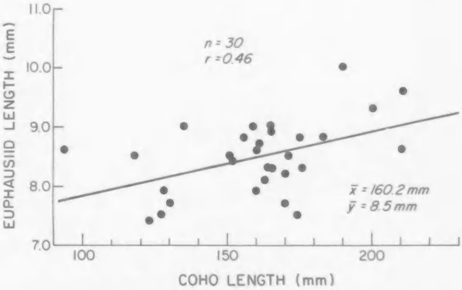


FIGURE 2.—The relationship between coho length and mean euphausiid prey length.

TABLE 3.—Frequency of occurrence (f/n %) and average abundance ($\bar{x}$) of prey found in stomachs of juvenile chum, coho, and chinook salmon.

	Chum		Coho		Chinook	
Prey taxa	f/n %	$\bar{x}$	f/n %	$\bar{x}$	f/n %	$\bar{x}$
Euphausiids						
Thysanoëssa spinifera (9 mm)	83	44.1	56	2.0	53	80.9
T. spinifera (22 mm)	2	2.0	15	2.2	5	1.9
Euphausia pacifica (18 mm)	2	1.0	8	2.0	3	14.5
Unidentified	10	12.7			5	4.3
Amphipods						
Parathemisto pacifica	15	1.2			8	1.6
Hyperoche medusarum	34	46.7			20	42.2
Primno macropa					2	1.0
Unidentified Hyperiidae	15	7.8	44	30.1	19	35.7
Gammaridae (*Atylus tridens*)			11	5.0	12	2.1
Fishes						
Ammodytidae						
Ammodytes hexapterus	10	1.2	30	2.4	32	2.0
Pleuronectiformes						
Isopsetta isolepis			1	1.0		
Citharichthys spp.			1	1.3		
Psettichthys melanostictus			1	1.0		
Unidentified flatfish			8	1.8	32	7.8
Hexagrammidae			3	1.6		
Gadidae			1	1.3	2	1.3
Cottidae					11	1.8
Hemilepidotus spp.			3	4.8		
Unidentified			3	1.6		
Clupeidae			6	3.1	3	2.2
Osmeridae			5	3.2	3	3.0
Scorpaenidae						
Sebastes spp.			15	3.5	8	1.4
Unidentified and Digested	10	2.5	45	3.1	48	1.7
Crab Larvae						
Cancer magister megalopae			16	4.2	9	1.8
Cancer spp. megalopae			16	0.6		
Pinnotheridae zoeae			10	4.7	3	19.2
Pinnotheridae megalopae					12	16.2
Paguridae zoeae					3	2.0
Copepods						
Calanus cristatus			6	8.1	1	12.0
C. marshallae			4	2.0		
Eucalanus bungii			4	1.0		
Epilabidocera longipedata			1	1.0		
Unidentified	12	1.6			3	1.0
Molluscs						
Limacina helicina			7	10.6	2	1.7
Cephalopods					1	1.0
Miscellaneous Arthropods						
Juvenile Crabs					4	14.0
Decapod shrimp mysis	2	2.0	6	2.5	6	1.0
Pandalus jordani zoeae			4	1.0	3	1.3
Barnacle cyprids	2	1.0	7	4.4		
Mysids			3	1.2	2	1.3
Insects	2	1.0	2	1.2	1	1.0
Chaetognatha						
Sagitta elegans	2	5.0	1	1.0		
Polychaetes						
Tomopteris sp.			1	6.5		

TABLE 4.—Frequency distribution of lengths of fish prey found in stomachs of juvenile coho salmon of various lengths.

Standard length of coho (mm)	Number of coho	Length of fish prey (mm)						
		0-10	11-20	21-30	31-40	41-50	51-60	>60
81-100	1		1	1				
101-120	3		3	1				
121-140	36	3	7	10	1	4		
141-160	66		27	35	4	4	1	1
161-180	70	8	69	80	28	21	2	
181-200	30		5	25	23	3	4	
201-220	7			7		1	1	

nile coho with stomachs full of fresh material to minimize the problem of differential digestion rates of various prey items. No statistically significant differences ($P>0.05$) were found between length of coho and either number of euphausiids, total number of prey items, or numbers of fishes. Significantly greater numbers of hyperiid amphipods occurred, however, in larger than in smaller coho (Fig. 3). Average weight of fishes in stomachs also increased with length of juvenile coho. Total weight of stomach contents was related to length of juvenile coho (weight of prey $= -1.0 + 0.016 \times$ length of coho, $r = 0.43$, $P<0.01$). The relationship between the two food groups most important to juvenile coho was investigated by plotting weights of euphausiids versus weights of fishes in the stomachs for each of the 87 coho. This plot was divided into quadrants by drawing lines parallel to the abscissa and ordinate at the median values of euphausiid and fish weight. The numbers of data points in each quadrant are shown in a 2×2 contingency table (Table 5). The χ^2 of 12.5 was highly significant ($P<0.01$, 1 df), indicating a strong tendency for juvenile coho to contain large amounts by weight of either fishes or euphausiids, but not both at the same time. Of these 87 coho, 26% contained only fishes and 21% only euphausiids. This trend may be a result of active selection of one type of prey or a result of prey patchiness. The latter explanation may be more plausible, since stratification of these two prey groups in the stomachs was evident in those individuals containing both prey items.

TABLE 5.—Contingency table comparing weight of fish and euphausiid prey found in the stomachs of 87 juvenile coho salmon.

		Euphausiid prey (g)	
		<0.24	>0.24
Fish prey (g)	>0.48	31	13
	<0.48	13	30

Variability in the composition of stomach contents of coho salmon was often high among the 10 stations where at least six fish were analyzed per station (Table 6). For example, juvenile euphausiids were the most numerically abundant prey taxa at four stations (2, 3, 12, and 29); hyperiid amphipods at four other stations (10, 27, 28, and 39); and fishes and crab larvae at one station each. The differences in feeding habits among stations were compared by calculating similarity indices for all possible station pairs. We used the percent similarity index (PSI $= \Sigma \min P_i$), where

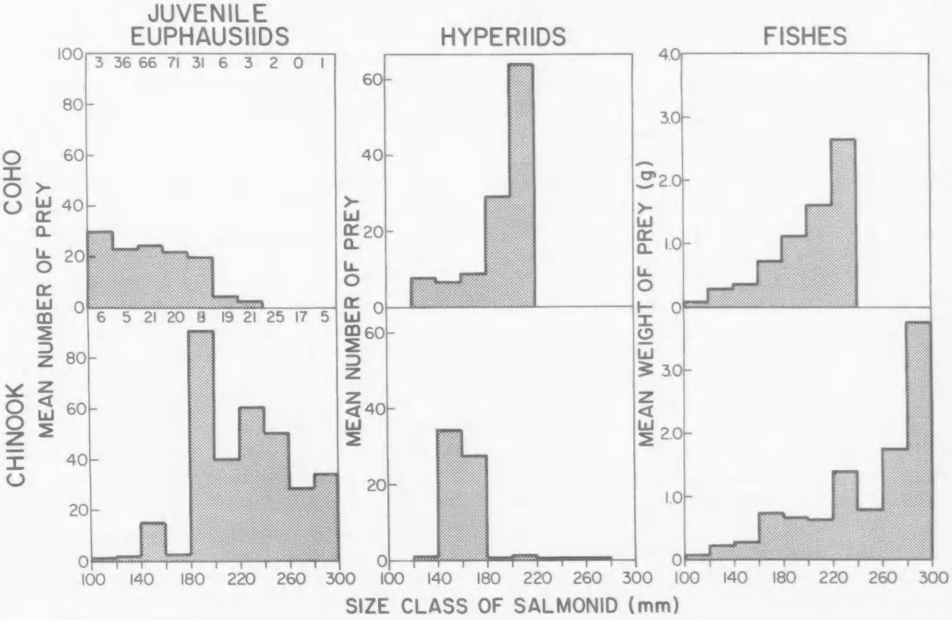


FIGURE 3.—Average abundance of juvenile euphausiids and hyperiids and average weight of fish prey occurring in the stomachs of each 20 mm size class of juvenile coho and chinook salmon. The averages are taken over only those stomachs in which prey items occurred. The numbers at the top of the leftmost figure denote the sample size in each 20 mm size class.

TABLE 6.—Sampling data and percent of total numbers of major prey items found in juvenile coho stomachs off the Oregon coast (only at those stations where six or more juvenile coho were taken). Includes only those prey taxa comprising 2% or more of the total number of prey items.

	Northern Oregon						Central Oregon			
Station	1	2	3	10	12	22	27	28	29	39
Time of day	0630	0900	1000	1730	0800	1500	0930	1130	1300	0900
Day in June	18	18	18	19	20	21	23	23	23	27
Water depth (m)	40	77	102	66	77	130	55	77	73	55
Distance from shore (km)	11.8	19.4	25.9	13.3	19.1	33.3	10.0	16.3	27.0	9.4
Number of coho examined	33	14	16	32	37	30	8	6	11	8
Average length of coho (mm)	158	175	158	154	158	163	165	161	157	193
Percent of coho with empty or nearly empty stomachs	58	79	69	25	8	20	12	33	0	0
Thysanoëssa spinifera (juveniles)	8.9	68.3	41.4	6.3	93.4	12.1	9.8	2.6	53.5	3.4
Hyperiid amphipods	20.1	22.5	26.9	36.0		13.0	39.7	89.9	30.7	94.0
Fishes	42.0	2.9	8.4	10.7	6.0	8.4	29.3			
Crab megalops				16.5		26.1				
Crab zoea			4.0			24.0				
Pteropods									9.2	
Calanus cristatus							6.5		4.9	
Cancer magister megalops			4.9	17.0		4.9				
Gammarid amphipods			6.2			7.7				
T. spinifera (adult)	16.6	2.1								
Barnacle cyprids			3.1	9.3		2.2				
Euphausia pacifica	9.5		3.1							
Total number of prey items	169	378	227	364	2,516	1,135	174	306	1,745	1,326

P_i is the proportion of the ith taxa (based on numbers of individual prey) in a stomach (Whittaker 1960), and PSI between a pair of stations is calculated by summing the smaller (minimum) P_i's for all food items. Similarity was generally low (<50%) among stations. Only 6 of the 45 possible pairings showed similarities >66% (stations 2-3, 2-12, 2-29, 3-29, 10-27, and 28-39), and only two pairs had a similarity >75% (2-29 and 28-39).

Some of this variability among stations may be related to the geographical regions sampled. For example, the numerical percentage of euphausiids averaged 45.5% for coho caught near the Columbia River plume (stations 1-22) compared with 17.4% off the central Oregon coast (stations 27-39, Table 6). Fishes occurred in the diets at all stations and made up 14% of the total prey numbers in the Columbia River area, whereas they were a significant part of coho diets at only one of four stations off Newport. Amphipods occurred more frequently in the stomach contents off Newport, averaging 63.6% of the total number, compared with 20.1% in coho from the Columbia River plume. The copepod, *Calanus cristatus*, and pteropod, *Limacina helicina*, were important components of the diets of only those juvenile coho caught off the central Oregon coast. An additional component of among-station variability may be attributed to differences in diet between inshore and offshore stations. Coho taken within 12 km of shore contained a greater proportion of fishes at two of three stations, while those captured offshore contained more euphausiids.

Chinook Salmon

Thirty taxa were identified from the stomachs of juvenile chinook. Major prey items were juvenile euphausiids (*T. spinifera*), hyperiid amphipods (mostly *Hyperoche medusarum*), pinnotherid crab larvae, and various fishes (Table 3). The most frequently identified fishes were flatfish and Pacific sand lance larvae, both occurring in 31% of the stomachs. Juvenile scorpaenids were third, occurring in only 7% of the stomachs.

Chinook salmon with stomachs full of fresh food ($n = 42$) were studied to test the hypothesis that weight of euphausiids and weight of fish prey in stomachs were independent, using the same procedure as with coho. The χ^2 from the contingency table (Table 7) was significant at the 0.07 level. Hence there is a tendency for chinook to eat either euphausiids or fishes, but this inverse relationship is not as strong as for juvenile coho salmon. The weight of stomach contents increased with size of juvenile chinook salmon. The slope of the regression (weight of prey = $-4.2 + 0.032 \times$ length of chinook, over the range of 100-200 mm) was significantly different from zero ($r = 0.66$, $P<0.05$).

TABLE 7.—Contingency table comparing weight of fish and euphausiid prey found in the stomachs of 42 juvenile chinook salmon.

		Euphausiid prey (g)	
		= 0.0	>0.0
Fish prey (g)	>0.67	14	7
	<0.67	7	14

Based on the percent by number, euphausiids and fishes were more important in the diet of chinook collected off the Columbia River than off the central Oregon coast (Table 8). As with coho, between-station variability was high. Only three station pairs had high similarities in diet (PSI >90%: 11-12, 11-14, and 12-14) mainly due to the high proportions of *T. spinifera* consumed at these stations.

Diet Overlap

Similarity (PSI) was calculated as before to study diet overlap among species of juvenile salmon at four stations where at least eight individuals of two or more salmon species occurred. Diets were similar (PSI >66%) at three of these stations. At station 12, chum, coho, and chinook juveniles ate 94.7, 93.4, and 90.9% euphausiids, respectively, by number; at station 27, coho and chinook ate nearly equal proportions of hyperiids and fishes; and at station 39, coho and chinook ate 94.0 and 91.3% hyperiids, respectively. Diets were dissimilar at station 1.

This dietary overlap among cooccurring species of juvenile salmonids suggests that a potential exists for competition, should food be limiting. This potential was highest among different size classes of juvenile coho and chinook salmon but was reduced among similar-sized fishes (Fig. 3). Euphausiids were eaten most often by coho 100-200 mm long, but not by chinook <180 mm. The opposite pattern is seen with hyperiid amphipods: Small chinook (<180 mm) ate more hyperiids than similar-sized coho. As juvenile salmonids of both species increased in length, they consumed larger fish, but coho between 140 and 330 mm consumed larger fish on the average than chinook of the same size. Juvenile chinook also consumed more pleuronectid larvae and fewer scorpaenids than coho. Chinook ate very few pteropods and no barnacle cyprids while these taxa occurred in about 10% of the coho stomachs (Table 3).

DISCUSSION

Fishes, euphausiids, hyperiid amphipods, and crab larvae were the most important prey for juvenile salmon off Oregon. Other published studies dealing with the diet of juvenile salmonids in the ocean show basically the same result, although there are notable differences. Manzer (1969) concluded that juvenile chum salmon from Chatham Sound, British Columbia, were planktivorous, feeding mostly on larvaceans (*Oikopleura* spp.) and unidentified copepods, and that coho were piscivorous, feeding mostly on Pacific herring and sand lance. Healey (1980) found that juvenile chum salmon from Saanich Inlet also fed predominantly on larvaceans and copepods, but individuals caught in more open waters of Georgia Strait ate euphausiids, amphipods, and fishes, as found off Oregon in this study. Juvenile coho studied by Healey contained 34% fishes (by volume) in Georgia Strait and 3% in Saanich Inlet, appreciably less than the 70% reported by Manzer in Chatham Sound. Healey concluded that chinook and coho from Georgia Strait had very similar food habits. Fresh et al.

TABLE 8.—Sampling data and percent of total numbers of major prey items found in juvenile chinook stomachs off the Oregon coast (only at those stations where six or more individual chinook were taken). Includes only those prey taxa comprising at least 2% of the total number of prey items.

	Northern Oregon						Central Oregon		
Station	1	8	11	12	14	18	27	39	43
Time of day	0630	1415	1915	0800	1055	1000	0930	0900	0410
Day in June	18	19	19	20	20	21	23	27	28
Water depth (m)	40	38	68	77	71	73	55	55	57
Distance from shore (km)	11.8	11.1	17.2	19.1	18.9	17.6	10.0	9.4	9.3
Number of chinook examined	8	9	12	14	13	14	19	11	6
Average length of chinook (mm)	147	208	239	253	211	245	183	164	178
Percent of chinook with empty or nearly empty stomachs	50	11	0	36	15	29	47	27	17
Thysanoëssa spinifera (juveniles)			97.2	90.9	98.9	22.8			46.4
Hyperiid amphipods		68.1				5.4	37.8	91.3	23.7
Fishes	30.1	25.3		8.3		45.7	19.9		13.4
Crab megalops	2.5	2.1				10.9	7.9	7.5	
Pteropods							31.6		
Euphausia pacifica	61.5								
T. spinifera (adults)	2.5					4.3			
Atylus tridens		2.1				3.2			
Calanus cristatus									12.4
Unidentified items	2.5								
Total number of prey items	39	185	1,906	277	1,846	92	291	987	97

(1981) reported that juvenile chum from nearshore pelagic habitats of Puget Sound fed on euphausiids, crab larvae, and gammarid amphipods on a weight basis; coho fed largely on larvae of decapod crustaceans; and chinook fed on euphausiids.

The qualitative range in variability of diet present during our 2-wk sampling period was similar to that found by the above authors from various months, years, and geographical locations. At some times and locations, euphausiids were dominant prey; at others, amphipods and fishes. This variability suggests that juvenile salmon are opportunistic, feeding on abundant prey available at a particular time and place.

The main prey items of our juvenile salmon comprise three general size groups: 1) Fishes having an average length of 29 mm, 2) euphausiids and *Cancer magister* megalopae, ranging in length from 7 to 10 mm, and 3) hyperiid amphipods between 4 and 6 mm.The fact that juvenile salmonids ate large numbers of euphausiids agrees with what is known about the abundances of various-sized planktonic prey sampled in coastal waters of Oregon during period years (Table 9). Over the range of 7-10 mm, euphausiids were the most abundant prey item. Shrimp larvae and *C. magister* megalopae were abundant only during limited periods, usually only June.

The predominant euphausiid eaten was *T. spinifera*, a neritic species. *Euphausia pacifica*, although a more abundant species of euphausiid in the North Pacific, is more oceanic and is not common in shallow shelf waters (Hebard 1966; Peterson and Miller 1976; Youngbluth 1976) and was found in low numbers in our salmonid stomachs. Juvenile salmonids collected off Oregon fed predominantly on subadult individuals, possibly because adult euphausiids migrate into deeper waters during the day (Alton and Blackburn 1972) when salmon presumably feed. Subadult euphausiids are abundant in the upper 20 m of the water column during both day and night (Peterson[5]).

TABLE 9.—Abundance of salmonid prey averaged from plankton samples collected during June and July at stations located 1, 3, 5, and 10 mi off Newport, Oreg. Zooplankton are averaged over the years 1969-72 (Peterson and Miller 1976); crab larvae over the years 1969-71 (Lough 1975, 1976); and larval fish from 1971 only (Richardson and Pearcy 1977). Plankton tows are step-oblique through the entire water column, during daytime, using a 0.2 m diameter bongo net (0.24 mm mesh) for zooplankton and a 0.7 m bongo net (0.5 mm mesh) for fish larvae.

Prey taxa	Average no./m^3
Pinnotheridae megalopae	0.1-1
Cancer magister megalopae	1-8
Pagurus megalopae	10-20
Calanus cristatus	2.3
C. marshallae (*C5* + females)	50
Pteropods	14.3
Hyperiid amphipods	3.6
Decapod shrimp mysis	19.2
Chaetognaths	11.7
Thysanoëssa spinifera	6.8
Larval fish	1-2

The large numbers of hyperiid amphipods and the paucity of copepods in the diet of juvenile salmon were surprising. Hyperiids are neither abundant in Oregon coastal waters nor are they particularly large compared with other more common planktonic taxa (Table 9). The average length of the amphipods (4.5 mm) is not much greater than *Calanus marshallae* (stage 5 copepodites and females, 3.0-4.0 mm TL (total length)). The ratio of amphipods to C5 *C. marshallae* abundance was 1:14 in plankton samples (Table 9) but 4:1 in the stomachs of juvenile coho. Frequency of occurrence in juvenile coho stomachs was 44% for amphipods compared with only 6% for *Calanus*. Similarly, the copepod *C. cristatus* (8 mm TL), with an average abundance about the same as hyperiids, was seldom eaten. Length alone may not be adequate for assessing size-selective predation in juvenile salmon. Okada and Taniguchi (1971) found that the upper size limit of prey may be determined by prey width. This may be relevant because hyperiids are generally much broader at their widest dimension than copepods of the same length.

One hypothesis to explain the high selectivity of amphipods by juvenile coho salmon concerns their peculiar swimming behavior and pigmentation. In the laboratory, hyperiids caught in coastal waters were extremely active swimmers (Peterson[6]). Most species have a large, heavily pigmented (black) compound eye, which could increase their detection by a visual predator, as shown for freshwater fish (Zaret and Kerfoot 1975). Copepods, on the other hand, lack the visual contrast of amphipods and are less active swimmers, generally swimming upwards and then sinking passively through a portion of the water column.

---

[5] W. T. Peterson, Marine Sciences Research Center, State University of New York-Stony Brook, Stony Brook, NY 11794, unpubl. data, 1977.

[6] W. T. Peterson, Marine Sciences Research Center, State University of New York-Stony Brook, Stony Brook, NY 11794, pers. obs. 1978.

Another explanation for the presence of large numbers of hyperiids in salmonid guts is that juvenile salmon may pick them from the surface of medusae. The predominant hyperiid consumed by chinook and chum salmon was *Hyperoche medusarum*, a species known to live on the exumbrellar surface of medusae (Bowman et al. 1963; Harbison et al. 1977). The host may be easy for salmon to locate, particularly the large *Chrysaora fuscescens* (bell diameter of several tens of centimeters), which were very numerous in our purse seine samples.

Larval fishes were the other important prey item. Information on their distribution and abundance is limited to sampling done in 1971-72. Data given in Table 9 are from Richardson and Pearcy (1977) for larvae captured at stations within 2-28 km from shore. Abundances were 200-400 larvae/10 m^2, or 1-2 larvae/m^3, assuming they are all distributed only within the upper 20 m of the water column.

To investigate the question of food limitation, estimates are needed of salmonid feeding rates, salmonid abundance, prey abundance, and prey population growth rates. Feeding and digestive rates can be inferred from field data, if there is pronounced diel periodicity in stomach fullness or state of digestion (Eggers 1977; Lane et al. 1979), but we have no evidence for this in our limited study. Thus, whereas estimates of stomach fullness were obtained from this study, feeding rates were estimated from other studies. The average weight of food in full juvenile coho stomachs (1.5 g wet weight) is equivalent to about 2.6% of the 55 g body weight of an average juvenile coho (160 mm long) (from Healey 1980). Walters et al. (1978, fig. 6) showed that the maximum ration of juvenile sockeye salmon weighing 55 g is slightly <3% of body weight per day. On the other hand, Brett (1971) found that the maximum daily intake of food was 7-8% of body weight for a 50 g sockeye salmon. Therefore, we assume that juvenile coho fill their stomachs between 1 and 3 times per day on the average.

Averaged over the 2-wk period in June 1979, the average 160 mm juvenile coho contained 37 euphausiids, 28 amphipods, and 4 fish (Table 1). In order to locate this quantity of food, this salmon would have had to search a minimum of approximately 5.4 m^3 of water for the euphausiids, 7.8 m^3 for the amphipods, and at least 4.0 m^3 for the larval fish. This assumes that all prey available to plankton nets are also fully available to juvenile salmon, and that annual differences are minor. Considering the well-known problems of zooplankton sampling variability and the fact that samples from different years are being compared, the agreement on water volume searched by salmon to locate each prey item seems quite good.

The maximum abundance of juvenile salmonids in any one purse seine was 123 fish, and the average number of fish in sets in which at least 5 fish were caught was 26. The mean abundance in these 16 sets was 17 fish/$10^5 m^3$. Juvenile coho abundances were about one-half as great, 8.7 fish/$10^5 m^3$, or 1 fish/11,500 m^3. If a juvenile coho fills its gut once per day, it needs to eat all prey in about 4-8 m^3 water/d. Thus, as a rough average, one individual would consume at least 4/11,500-8/11,500 (or 0.03-0.07%) of the available prey per day. Should this individual coho fill its gut three times each day, it would consume up to 0.1-0.2% of the standing stock of prey per day. Coho and chinook combined would consume about 0.2-0.4% of available prey per day. If growth rates of prey population equal or exceed these loss rates, predation by juvenile coho and chinook alone will not reduce standing stocks of prey. Unfortunately, estimates of these vital parameters are lacking.

Walters et al. (1978) examined the effect of food limitation on juvenile salmon growth and survival using a computer simulation model. Input variables included 1) zooplankton distribution, abundance, and production rates; 2) ration, growth, and mortality of young salmon in relation to body size; and 3) timing of arrival of smolts at sea and rate of migration along the coast in relation to zooplankton production cycles. They tentatively concluded that juvenile salmonids were not food-limited, but rather predator-limited. This conclusion rests on a crucial assumption of the availability of zooplankton prey, which may be in error. Their estimates of zooplankton production and mortality and fish consumption (their table 3, columns 5, 6, and 7) were calculated using estimates of the biomass of zooplankton within a 20-400 m water column, despite their assumption that salmon forage only in the upper 20 m of the water column. They assumed that zooplankton prey removed by salmon during the day will be replaced from deepwater zooplankton populations at night. Since the surface biomass is enhanced by diel vertical migrations mainly at night and juvenile salmonids are thought to be daylight or crepuscular feeders (see Bailey et al. 1975; Godin 1981 and references therein), they may never encounter this nighttime increase in zooplankton abundance.

The studies of Healey (1980) and Simenstad et al. (1980[7]) both suggest that food availability may affect the abundance of juvenile salmon. They found that fewer salmon remained in Georgia Strait (British Columbia) and Hood Canal (Washington), respectively, when feeding conditions were poor. Obviously, the question of ocean limitation of salmon production cannot be resolved until much more is learned about the ecology of juvenile salmon and their competitors in the coastal zone. Substantially more information is needed on the abundance and availability of prey in near-surface waters, as well as on feeding, growth rates, and migration patterns of juvenile salmon.

ACKNOWLEDGMENTS

This research was made possible by funding provided by the Oregon Department of Fish and Wildlife (ODFW), Pacific Marine Fisheries Commission, Oregon State Sea Grant College Program, Oregon Aqua-Foods Inc., Crown Zellerbach Inc., and Anadromous Inc. We are indebted to the Northwest and Alaska Fishery Center of the National Marine Fisheries Service for the loan of the purse seine. James Lichatowich, Thomas Nickelson, and Jay Nicholas (ODFW), Charles Simenstad (University of Washington), and two anonymous reviewers made helpful comments on the manuscript.

LITERATURE CITED

ALTON, M. S., AND C. J. BLACKBURN.
1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen, in coastal waters of Washington. Calif. Fish Game 58:179-190.

BAILEY, J. E., B. L. WING, AND C. R. MATTSON.
1975. Zooplankton abundance and feeding habits of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fish. Bull., U.S. 73:346-861.

BOWMAN, T. E., C. D. MEYERS, AND S. D. HICKS.
1963. Notes on associations between hyperiid amphipods and medusae in Chesapeake and Narragansett Bays and the Niantic River. Chesapeake Sci. 5:141-146.

BRETT, J. R.
1971. Satiation time, appetite, and maximum food intake of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28:409-415.

EGGERS, D. M.
1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34:290-294.

FRESH, K. L., R. D. CARDWELL, AND R. R. KOONS.
1981. Food habits of Pacific salmon, baitfish, and their potential competitors and predators in the marine waters of Washington, August 1978 to September 1979. Wash. Dep. Fish. Prog. Rep. 145, 58 p.

GODIN, J.-G. J.
1981. Daily patterns of feeding behavior, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia. Can. J. Fish. Aquat. Sci. 38:10-15.

HARBISON, G. R., D. C. BIGGS, AND L. P. MADIN.
1977. The associations of Amphipoda Hyperiidea with gelatinous zooplankton.—II. Associations with Cnidaria, Ctenophora, and Radiolaria. Deep-Sea Res. 24:465-488.

HEALEY, M. C.
1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, p. 203-229. Oreg. State Univ. Press, Corvallis.

HEBARD, J. F.
1966. Distribution of Euphausiacea and Copepoda off Oregon in relation to oceanographic conditions. Ph.D. Thesis, Oregon State Univ., Corvallis, 85 p.

LANE, E. D., M. C. S. KINGSLEY, AND D. E. THORNTON.
1979. Daily feeding and food conversion efficiency of the diamond turbot: an analysis based on field data. Trans. Am. Fish Soc. 108:530-535.

LOUGH, R. G.
1975. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Thesis, Oregon State Univ., Corvallis, 229 p.
1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-71. Fish. Bull., U.S. 74:353-376.

MANZER, J. I.
1969. Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. J. Fish. Res. Board Can. 26:2219-2223.

OKADA, S., AND A. TANIGUCHI.
1971. Size relationship between salmon juveniles in shore waters and their prey animals. Bull. Fac. Fish., Hokkaido Univ. 22:30-36.

PETERSON, W., AND C. MILLER.
1976. Zooplankton along the continental shelf off Newport, Oregon, 1969-1972: distribution, abundance, seasonal cycle and year-to-year variations. Oreg. State Univ. Sea Grant College Prog. Publ. ORESU-T-76-002, 111 p.

RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.

---

[7] Simenstad, C. A., W. J. Kinney, S. S. Parker, E. O. Salo, J. R. Cordell, and H. Buechner. 1980. Prey community structure and trophic ecology of outmigrating juvenile chum and pink salmon in Hood Canal, Washington. Final rep. (1977-79) No. FRI-UW-8026, 113 p. University of Washington, Fisheries Research Institute, Seattle, WA 98195.

WALTERS, C. J., R. HILBORN, R. M. PETERMAN, AND M. J. STALEY.
1978. Model for examining early ocean limitation of Pacific salmon production. J. Fish. Res. Board Can. 35: 1303-1315.
WHITTAKER, R. H.
1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30:279-338.
YOUNGBLUTH, M.
1976. Vertical distribution and diel migration of euphausiids in the central region of the California Current. Fish. Bull., U.S. 74:925-936.
ZARET, T. M., AND W. C. KERFOOT.
1975. Fish predation on *Bosmina longirostris*: Body-size selection *versus* visibility selection. Ecology 56:232-237.

SPAWNING AND LARVAL DEVELOPMENT OF THE HOGFISH, *LACHNOLAIMUS MAXIMUS* (PISCES: LABRIDAE)

PATRICK L. COLIN[1]

ABSTRACT

Spawning of the hogfish, *Lachnolaimus maximus*, along a reef-sand interface near the insular shelf edge off southwestern Puerto Rico was observed over a period of 20 months by scuba diving. Eggs were collected and returned to the laboratory for hatching. Male-female ratio was about 1:10. Males patrolled elongate territories, which did not change during the 20 months, during the afternoon. Males initiated spawning by a courtship display using the prolonged dorsal fin spines and other fins. If the female responded, an elaborate process, termed the spawning rush, occurred during which the gametes were released. A male spawned with one female at a time, but often spawned with several females during an afternoon. Peak spawning was from December to April. There was no evidence that spawning was influenced by current speed or direction or by lunar or tidal periodicity. Eggs were planktonic, about 1.2 mm in diameter, lacked visible pigment, and hatched in 23 hours at 25.5°C. They were preyed on extensively by yellowtail snappers, *Ocyurus chrysurus*. Larvae, which survived in the laboratory up to 50 days, lacked a distinct transformation to juveniles but gradually acquired pigment and juvenile form after 13 days. Free-swimming postlarvae formed mucous bubbles at night.

The hogfish, *Lachnolaimus maximus* (Walbaum), is the largest tropical western Atlantic labrid, reaching about 11 kg (Randall and Warmke 1967); adults are conspicuous members of many reef communities. A highly prized foodfish, it is taken incidentally with other fishes, particularly by spear or hook and line.

It is a protogynous hermaphrodite, but there are no primary males. Color patterns are distinctive between sexes. Males, which are more highly pigmented, have a dark reddish brown mask on the head. Also of the same hue are the base and first soft rays of the dorsal fin, the base of the rays in the lunate caudal fin, the pelvic fins, and the leading edge of the anal fin. The color of these darkened areas varies in intensity, depending on the nervous state of the male. The pectoral fins are yellow and there is an elongate spot on each side of the body. Females lack the reddish brown darkening, but possess a black spot about the size of the eye at the posterior base of the dorsal fin. The first three dorsal fin spines are greatly prolonged in males, much more than in females. Males also have filaments on the anal fin, soft dorsal fin, and margins of the caudal fin. The snout is longer in males and has a concave profile.

Although various aspects of its biology, such as food habits (Reid 1954; Randall and Warmke 1967; Davis 1976) and growth (Davis 1976), have been well documented, little has been published on spawning or early life history. While scuba diving on a shelf-edge coral reef off southwestern Puerto Rico to study reef fish spawning, I encountered a large spawning population of hogfish. I was able to observe the courtship display and spawning rush over a 20-mo period from December 1977 to July 1979. I also was able to collect large numbers of fertilized eggs, which were returned to the laboratory and hatched. A large number of larvae were kept alive up to 30 d, while smaller numbers were maintained to 50 d. I was able, therefore, to describe and illustrate in some detail the development of larvae from hatching through the juvenile stage.

METHODS

Observations of Courtship and Spawning

The site was visited 154 d during the 20 mo. From December through March, when spawning was high, visits were daily, if possible, but during the summer, visits were usually weekly.

Males and females were observed both at close range and also from the maximum distances possible. The presence of observers had less effect on

---

[1] Mid-Pacific Research Laboratory, c/o Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

Manuscript accepted February 1982.

the behavior of males than females, but no disturbance was noted if the observer moved no closer than about 4-8 m. Only during early phases of the spawning rush would rapid movements by a diver cause the female to abort the spawning rush. Once the spawning rush had reached an advanced point, however, the observer could approach quickly without interrupting. Fish frequently observed seemed to become accustomed to the observers.

Motion pictures (16 mm) were made of different aspects of spawning behavior. These were analyzed frame-by-frame to determine the duration of each act and the orientation of the fish during the rapid spawning rush.

Collection and Rearing of Eggs

Eggs were collected with fine mesh dip nets (sold as "brine shrimp nets") 10 by 15 cm with mesh openings of about 100 μ in diameter. After some practice, an observer could follow a pair on their spawning run and quickly locate the diffuse cloud of gametes when they were released. The cloud was either constantly observed or squirted with ink mixed with seawater from a plastic bottle to provide a reference mark. About 45 s to 1 min were needed to assure fertilization. After that time, eggs were collected by passing the net through the water where the eggs occurred. In one smooth motion, the net was then everted into a plastic bag and the bag was filled with water from the area where the gametes occurred, in hope of obtaining more sperm in the water and thereby increasing the chances of fertilization. Eggs collected before 45 s had elapsed generally were not fertile. Since the ability to see the cloud of gametes decreases with each second, the collection of planktonic eggs with a small hand net is a contest between the time required for fertilization and the ability of the collector to discern the location of the eggs. Although the ink helps to locate the eggs, it quickly disperses or tends to rise or sink because of the differences in density. I found it valuable to remain about 0.5-1.0 m away from the cloud, once it had been located, and focus on sediment particles, opaque eggs, or larger zooplankton rather than trying to follow the rapidly dispersing cloud. If the bag is clear plastic, the eggs, once inside, can be seen easily. It helps to face the sun (underwater) and backlight the eggs by blocking out the sun directly to the eyes with a hand behind the bag.

The eggs in the bags were transported to the laboratory in buckets partially filled with seawater, and were released into aerated closed-circuit 80 l aquaria within about 90 min of being collected. Rearing methods followed Houde and Tanaguchi (1977). The aquarium was constantly illuminated by a twin 20-watt fluorescent lamp. A culture of *Chlorella* was introduced at hatching. Later larvae were fed wild zooplankton collected with 53 μ mesh nets. Temperatures were maintained at 25°-27°C.

Selected eggs and larvae were preserved in 3% Formalin[2]. Larvae were illustrated from preserved specimens by a camera lucida attachment on a dissecting microscope.

The Study Site

The study site was located on the insular shelf edge 16 km ESE of La Parguera, Puerto Rico (approximate position: lat. 17°54′N, long. 66°57′W). It is typical of most reefs off the south coast of Puerto Rico and the Virgin Islands (MacIntyre 1972; Adey et al. 1977). It is an elevated ridge about 100-150 m wide, paralleling the actual shelf break, and has a rocky substrate with abundant coral, particularly on the seaward and inshore flanks. Minimum depth is about 16 m. Near the study area the seaward portion slopes gently to about 18-19 m depth, then plunges downward at an angle of about 60° to oceanic depths. The inshore side slopes downward at about 10° until it meets a nearly level sandy-rubble plain. This slope, termed the "moat slope," is where most spawning activity by *L. maximus* was observed.

Water temperatures varied between 24° and 27°C, visibility between 50 and 10 m. The area is within the trade wind belt of the Atlantic tropics and is consistently exposed to easterly winds of moderate force (Glynn 1973). Waves usually consisted of a small wind produced chop associated with larger swells. Wave heights of 1-2 m were common, but seldom exceeded 2 m. Complete calms would occasionally occur, most often during winter. These calms were associated with lee-shore conditions on the southwestern coast and occurred only a few percent of the time. Currents were generally east to west, paralleling the shelf edge, but occasionally they were completely reversed or ran strongly off or onto the shelf. Clearest water occurred when strong southeasterly winds drove oceanic water up onto the shelf edge and also produced rough conditions. The most turbid water was either associated with calms, when the normal wind-driven flow from offshore was eliminated, or when large amounts of rain fell on Puerto Rico, particularly during the summer-fall wet season.

---

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

OBSERVATIONS

Spawning Groups of *L. maximus*

Males established a territory along the moat-moat slope interface and defended it against the intrusion of other males. The territory was unusual in being very elongate along the moat-moat slope axis, but not ranging far either over the sandy moat or up the moat slope. Males patrolled their territory during the afternoon, passing from one extreme of the sand-reef border to the other without changing direction except as interrupted by spawning rushes with females. Three territories that I closely examined each encompassed about 100 m of the moat-moat slope interface. The turning points at either end remained consistent over the entire 20 mo. During active spawning periods, generally 2-3 min, were required for one "pass" if no spawning occurred.

An estimated 10-15 females occurred with each male during the afternoon. Although I found some evidence that females may remain with the same male during any one day, I could not determine if they changed males at other times.

Time and Conditions of Spawning

Active spawning was observed from December through April, but I could not be sure if spawning also occurred in other months when low water visibility often made observations difficult. Males, however, continued to patrol their territories during the afternoon and were occasionally seen to court females, but no spawning was seen. In any event, it is certain from direct observation that spawning during winter and spring must be at least an order of magnitude above any that may occur during summer and fall. Davis (1976) reported that peak spawning, based on gonad indices, of Florida Keys hogfish is probably in February and March, although some spawning may be occurring in other months. Gonad indices were consistently low from May through August.

There is no evidence for lunar periodicity. During peak spawning periods, spawning rushes occurred on all phases of the moon and spawning proceeded day after day with no apparent change over the lunar cycle.

Spawning began in midafternoon, but the exact time of initiation was never observed. Hogfish were spawning by 1.5 h before sunset and continued to spawn until 15-30 min before sunset. Males began to patrol more slowly as sunset approached, and the frequency of spawning rushes decreased quickly. Females seemed to leave the spawning area, or at least were not visible, by about 15 min before sunset. Males continued to patrol slowly until about sunset, then left the immediate area of the sand-reef interface.

During the season of active spawning, current speed or direction, surge on the bottom, and water clarity seemed to have little effect on spawning behavior. Rushes were observed under nearly all conditions encountered. Water temperatures ranged between 24° and 26°C. Day length was short, being near the annual minimum of about 11 h near the start of peak spawning in December and about 12.5 h by April.

Spawning Behavior

A female often indicated her readiness to spawn by moving up in the water column on approach of a male; otherwise, a male would actively court females encountered on his patrol. If a female was seen near the bottom, a male would swim quickly towards her, shifting from pectoral sculling to caudal fin swimming in a burst of speed, and then dive towards her exhibiting a courtship display. This consisted of erecting the three long anterior spines of the dorsal fin and shaking the posterior two of these rapidly back and forth at about 8-10 cycles/s. The posterior portion of the dorsal fin, the upper and lower caudal fin margins, and the pelvin fins were also agitated at a similar rate. Often the male would swoop above the female and dive rapidly towards her while displaying. If no response was elicited, the male would move quickly on to another female or resume patrolling.

The spawning act was part of an elaborate process termed the spawning rush, which could be initiated by the male actively courting the female or by the female simply rising up in the water column as the male approached on his patrol. The rush required 10-25 s total time from the time the fish left the vicinity of the substrate.

On the basis of hundreds of observations and the complete filming of 12 rushes, the spawning rush may be broken down into six distinct periods: 1) Pectoral swim up, 2) tail swim, 3) swim alongside and tilt, 4) release, 5) circle and display, and 6) swim down (Fig. 1).

1) Pectoral swim up—A male approaching from some distance a female which was up above the bottom would swim upward at an angle of 10°-20° towards the female, using concurrent sculling of the pectoral fins, usually of 2.0-2.5 beats/s. The dorsal and anal fins were folded against the body. As he approached the female, who rose slowly at a steeper angle to match his ascent, the male began to turn laterally and shifted to the second type of swimming.

2) Tail swim—The male folded the pectoral fins against his body and began undulating the caudal fin and posterior portion of his body at about 4 beats/s. Pelvic fins were usually about one-half extended. The female continued to rise slowly as the male approached her from behind. This stage lasted about 2-5 s.

3) Swim alongside and tilt—The male, using the tail only, continued swimming and came forward alongside the female, who was still moving forward. Their bodies were close together, the male slightly behind the female with his snout about even with her eye (Fig. 2). Once alongside, the male angled the dorsal portion of his body outward at about 15°-20° from the female. This took 0.5-1.5 s. During this phase, the male and female turned laterally 90°-180° in the direction of the female.

4) Release—At the end of the turn to initiate gamete release, the male started swimming forward more rapidly than the female. As he overtook her, he bent his body laterally towards her, then broke in the opposite direction. At this time the gametes of both sexes appeared to be released. The cloud could usually be seen, but the exact moment of release was difficult to determine. In some cases the male, when he turned toward the female, was sufficiently far forward to actually cross slightly into her path. The sharp break away from the female was accomplished by a sharp flick of the caudal fin. This also served

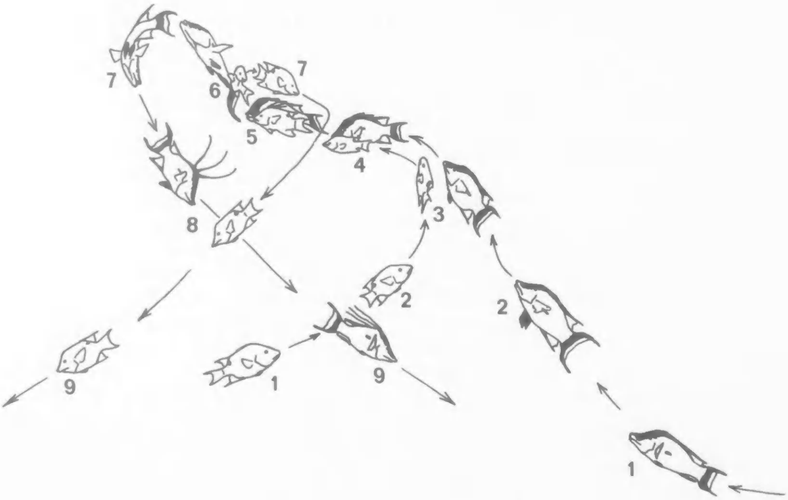


FIGURE 1.—Idealized spawning sequence of *Lachnolaimus maximus* under conditions where the female meets the male in midwater. The male (right) approaches and initiates the "pectoral swim up" action (1) followed by "tail swim" (2-3) when approaching the female. The lateral turn in "swim alongside and tilt" towards the female (4-5) is followed by the "release" of the gametes (6). "Circle and display" (7-8) precedes "swim down" (9). In this case the male is illustrated as returning in the direction opposite that when spawning was initiated, but this is not always the case. Often the male will continue patrolling in the same direction.

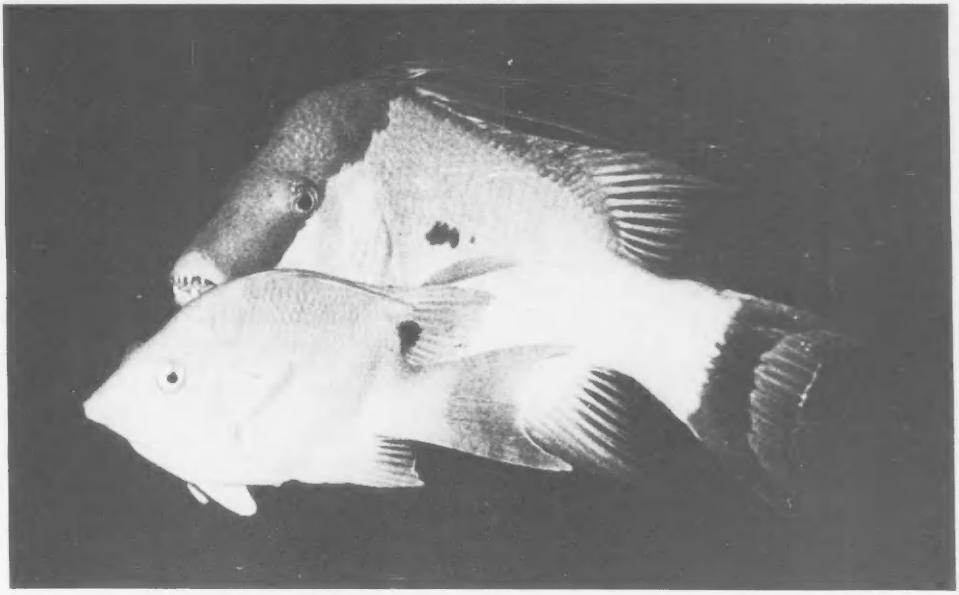


FIGURE 2.—Photograph of spawning pair of *Lachnolaimus maximus* with the smaller female in front of the male. The fish are turning laterally in the "swim alongside and tilt" action just prior to release of the gametes. Photo by C. Arneson at the study site.

to create a turbulent eddy where the gametes had been released to aid in their mixing.

5) Circle and display—When the male broke sharply away from the female, she also turned away, but not as sharply. Both started downward, the male doing a 180° lateral turn while descending. When laterally exposed to the female he initiated a display similar to that used in courtship. The three dorsal spines were erected, the last two shaken. The soft portion of the dorsal and anal fins, the upper and lower margins of the caudal fin, and the pelvic fins were agitated at a rate of 8-10 times/s. This display continued for 1-3 s as the male approached the female and they continued down.

6) Swim down—The male separated from the female and swam downward at a steep angle. She did likewise. He may quickly approach another female and engage in courtship behavior or he may simply rise into the water column if another female is ready to spawn. Occasionally he will court the female he has just spawned with after they have returned to near the substrate, but I have never seen a female spawn two times in rapid succession.

In many instances it was possible to observe the gamete cloud after it had been released. The movements of the fish, particularly the male, produce an area of turbulence where the gametes are thoroughly mixed. On occasion the actual sperm cloud was also faintly visible. Within 15-20 s after release, the gametes will occupy a volume near 1 m^3. There are usually several hundred or more eggs released per rush. In some instances no egg cloud could be found, even though the usual procedures for locating it were followed and the observer arrived within a few seconds to the region in which the eggs should have been. It is possible, but not yet proven, that eggs are simply not released on some rushes.

Yellowtail snappers, *Ocyurus chrysurus*, were active predators on the eggs immediately after release. One to as many as ten yellowtail snappers would converge on the egg cloud 1-2 s after eggs had been released and would pick individual items, presumably eggs, from the water. This occurred in about 20-40% of rushes. Generally if yellowtail snappers observed a pair of *L. maximus* rising to spawn, they would attempt to locate and eat the eggs. On occasion individuals would follow pairs of *L. maximus* so closely that the spawning rush would be interrupted, causing both the male and female to return to the substrate.

Yellowtail snappers were much more abundant at the actual insular shelf edge than at the hogfish spawning area. At the shelf edge they formed loose aggregations of from several hundred to several thousand individuals feeding on zooplankton high above and beyond the shelf edge. Only a relatively few were found near the moat-moat slope interface, some 100 m away, but these few influenced the reproductive success of *L. maximus.*

Gonad indices of both sexes vary considerably during the year (Davis 1976) in a pattern consistent with my observations. Gonad indices of males for each month ranged from about 0.14 to 0.20 (gonad weight as a percentage of body weight) for December to April and from 0.0 to slightly less than 0.10 for June to August. The indices were relatively low compared with those for other Caribbean labrids (Warner and Robertson 1978) but on a level with those of terminal males (both primary and secondary) of some other species. *Lachnolaimus maximus* is monandric (no primary males) (Davis 1976) and haremic, and the low gonad indices of males are consistent with the data for larger Caribbean labrids of Warner and Robertson (1978). Males are close to an order of magnitude heavier than other "large" Caribbean labrid males (*Halichoeres radiatus* and *Bodianus rufus*) and two orders of magnitude above those of smaller species. Although the gonad indices are low compared with those of other species, the actual gonad is large. The relative size between large and small labrids may not be very important. Males observed in the present study spawned repeatedly each afternoon during the active season. While data for an entire afternoon were not available, I estimated that at least some males engaged in 50-100 spawning rushes/afternoon and that they were capable of fertilizing each group of eggs released.

The female-male ratio among adults also seems higher than in most other Caribbean labrids. Davis (1976) reported a ratio of 13:1 in the 724 individuals he sampled, which is close to the estimated 10:1 ratio that I observed. Warner and Robertson (1978), however, reported a ratio of only 3:1 or less for most species.

The spawning location, about 100 m from the insular shelf edge rather than at the edge itself, appears contrary to some of the concepts put forward by Johannes (1978). It is true that many reef fishes producing planktonic eggs often move considerable distances to be able to release eggs at insular shelf edges where they may be transported offshore. Hogfish, however, rarely move long distances to spawn. Adults can easily range to the shelf edge for spawning and some individuals probably remain along the shelf edge at night after spawning ceases. The potentially heavier egg predation by yellowtail snapper at the shelf edge may help restrict hogfish spawning to more inshore areas. In addition, hogfish are typically found on the sandy margins of reefs where they feed largely on sand-dwelling molluscs (Randall and Warmke 1967) and the moat-moat slope interface area provides both reef shelter and open sand. Territories held by males may also represent feeding areas, whereas the actual shelf edge near the spawning area has little sand, and consists mostly of rock and coral.

EGG AND LARVAL DEVELOPMENT

Eggs are 1.2 mm in diameter and have a single oil globule 0.17 mm in diameter. They float and lack any visible pigment. They hatched 23 h after fertilization at 25.5°C.

Larvae were reared at about 26°C but the temperature could not be closely controlled. When hatched, the larvae had little pigment. Scattered melanophores occurred in the head region and in a line on the dorsal margin of the body (Fig. 3a). They did not orient until about 24 h after hatch, but the eyes were still unpigmented at that stage (Fig. 3b). A line of melanophores along the ventral surface of the body began to develop at this time. Sometime between 24 and 36 h posthatch the eyes became pigmented. First food was added 31 h after hatch. Larvae seemed to be making feeding strikes by about 42 h posthatch (Fig. 3c). At this stage the amount of pigment along the ventral surface of the body increased and was plainly visible to the unaided eye. The black pigment increased daily until 7-8 d posthatch and then remained stable. At 7 d posthatch feeding with *Artemia salina* was initiated. At this time pigment cells were visible on the tip of the lower jaw and on the lower margin of the gill cover. By 10 d posthatch the fin rays had begun to develop, the pelvic fin buds were apparent, and notochord flexion had occurred.

Gas bladder inflation occurred 10 d posthatch (Fig. 3e) in 10-20% of the larvae. Larvae without the bladder inflated would swim with the tail

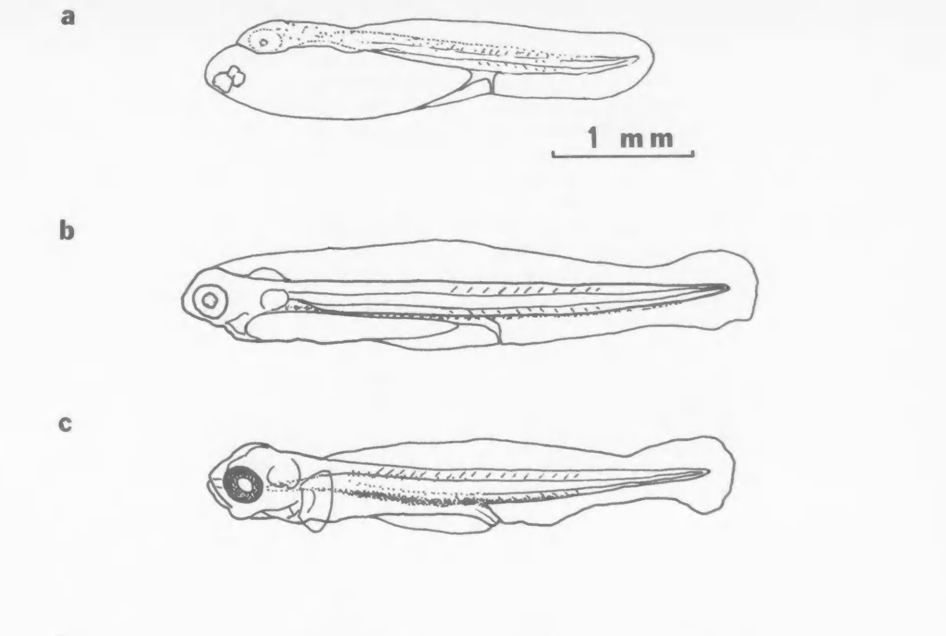


FIGURE 3.—Larval stages of *Lachnolaimus maximus*. a, At hatch; b, 24 h posthatch; c, 42 h posthatch; d, 7 d posthatch; e, 10 d posthatch.

down at an angle of 20°-30° while those with the bladder inflated would swim with the tail slightly up. By 12-13 d the bladders of nearly all larvae had been inflated.

At 13 d posthatch the first traces of the juvenile color pattern began to appear (Fig. 4a) with the development of three pigmented lobes on the base of the anal fin. Widely scattered brown chromatophores appeared on the body, but showed no discernible pattern. At this point the full complement of dorsal, anal, and caudal fin rays had been developed, but the pectoral rays did not seem fully developed. The pelvic fins consisted of only a slight bulge and the first three spines of the dorsal fin were elongated compared with those more posterior. At this stage the fish were considered to be postlarvae.

At 17 d the body had a distinct brown and white color pattern (Fig. 4b) with the first three dorsal spines elongated. At this stage there was little difficulty identifying the postlarvae as *L. maximus*. The postlarvae did not orient to the bottom of the rearing tank, but remained free-swimming. The lights of the rearing tank were extinguished for the first time overnight at 17 d posthatch. Over one-half of the larvae formed

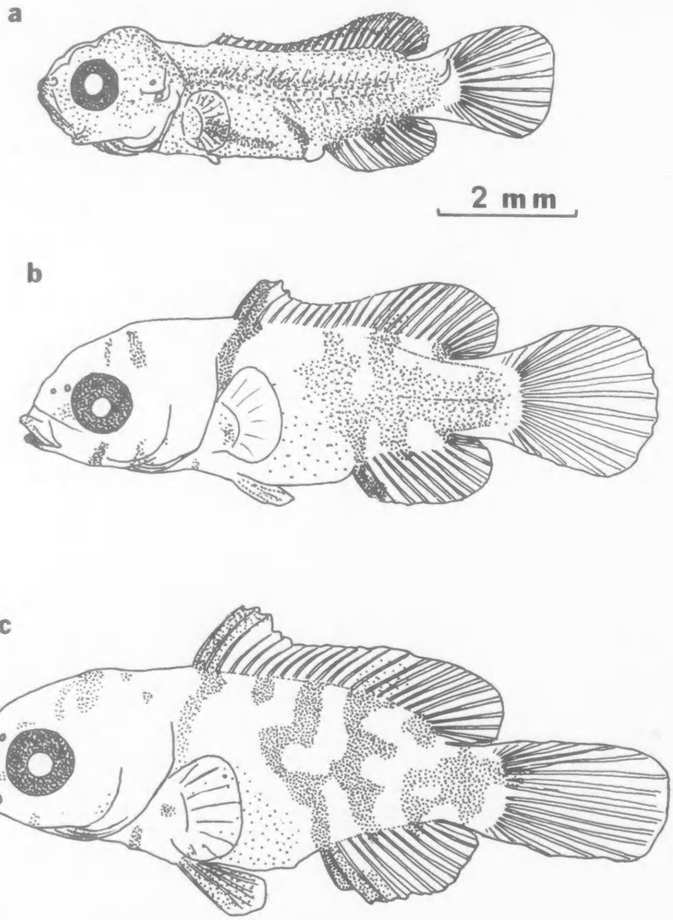


FIGURE 4.—Larval stages of *Lachnolaimus maximus*. a, 13 d posthatch; b, 17 d posthatch; c, 25 d posthatch.

mucous bubbles around themselves that night while floating free in the water near the surface. None rested on the bottom. Such behavior is known in other labrids but had been previously unknown for *L. maximus* or among free-floating individuals. Adults have been observed many times at night with no mucous bubble formation. Bubble formation has not been previously noted for "nonbenthic" labrids. The concept of bubble formation as an antipredator device is supported by its occurrence in postlarvae. Most larvae broke free of the bubbles within seconds after lights were turned on.

At 17 d posthatch, postlarvae tended to stay under material floating on the surface of the water (mostly discarded clumps of mucous bubbles and *Artemia* cysts). Several would stay under a single clump at the surface. No aggressive interactions were noted. Larvae were white and brown, the colors and pattern closely resembling that of *Sargassum*, which may serve as shelter for postlarvae carried into offshore waters.

Ten 18-d posthatch postlarvae were put into an 80 l aquarium with a white sand substrate. Some individuals rested on the bottom the first night, while others remained in the water column, all in mucous bubbles. By 34 d posthatch the fish oriented strongly to the bottom.

Little is known of the early life history of juveniles. Roessler (1964), who reported them from *Thalassia* beds, found some correlation in abundance with density of the bed. The larvae reared in the present study were maintained until about 50 d posthatch, but after about 30 d began dying without obvious cause. They were maintained either in bare aquaria or with a white sand bottom and were never exposed to a *Thalassia* community. They were fed a combination of *Artemia* and wild zooplankton. In their natural environment there may be a diet shift to microinvertebrates at an age when they began dying.

Larvae did not undergo a quick metamorphosis but gradually began to acquire brown and white pigment of juveniles about 13 d posthatch. While still free-swimming the larvae and postlarvae became highly pigmented, which would seem to be a distinct disadvantage in open water. These pigmented young seemed to shelter beneath any floating objects in the rearing aquarium, particularly the shards of their discarded mucous bubbles, which were brown in color. While there are no reports in the literature, their coloration would serve to conceal them in floating *Sargassum* and potentially other floating marine plants. Quick development and the lack of a distinct metamorphosis implies that perhaps the optimum survival strategy to the juvenile stage would be an inshore transport of eggs and larvae and retention of juveniles near the spawning location. Unless associated with floating objects or plants, large *L. maximus* larvae would be at a distinct disadvantage in the pelagic realm. The life history of *L. maximus* implies that the postlarvae become benthic in an inshore location near sea grass beds and subsequently move to offshore reefs (Davis 1976). From the present study there seems no control of spawning condition which would produce an inshore dispersal of eggs (currents, winds, tides, or wave action) and except for seasonal differences, it seems eggs are simply broadcast randomly without the influence of environmental conditions which would influence their ultimate destination.

ACKNOWLEDGMENTS

Major equipment was provided by two grants (OCE76-02352 and OCE78-25770) from the Division of Ocean Sciences, National Science Foundation, to the author. Much of the operational support was provided by two grants from the National Geographic Society. Ileana Clavijo and Charles Arneson participated in most of the field work. Charles Arneson provided Figure 2. Two journal reviewers provided valuable criticism of the manuscript.

LITERATURE CITED

ADEY, W. H., I. G. MACINTYRE, AND R. STUCKENRATH.
1977. Relict barrier reef system off St. Croix: Its implications with respect to late Cenozoic coral reef development in the western Atlantic. Proc. Third Int. Coral Reef Symp., Miami, 2:15-22.

DAVIS, C.
1976. Biology of the hogfish in the Florida Keys. M.S. Thesis, Univ. Miami, Coral Gables, 86 p.

GLYNN, P. W.
1973. Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: Part I. Meteorology and hydrography. Mar. Biol. (Berl.) 20:297-318.

HOUDE, E. D., AND K. TANAGUCHI.
1977. Methods used for rearing marine fish larvae at the Rosenstiel School of Marine and Atmospheric Sciences. Report to Environmental Protection Agency.

JOHANNES, R. E.
1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fishes 3:65-84.

MACINTYRE, I. G.
1972. Submerged reefs of eastern Caribbean. Bull.

Am. Assoc. Pet. Geol. 56:720-738.

RANDALL, J. E., AND G. L. WARMKE.
1967. The food habits of the hogfish (*Lachnolaimus maximus*), a labrid fish from the western Atlantic. Caribb. J. Sci. 7:141-144.

REID, G. K., JR.
1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4:1-94.

ROESSLER, M.
1964. A statistical analysis of the variability of fish populations taken by otter trawling in Biscayne Bay, Florida. M.S. Thesis, Univ. Miami, Coral Gables, 126 p.

WARNER, R. R., AND D. R. ROBERTSON.
1978. Sexual patterns in the labroid fishes of the western Caribbean, I: The wrasses (Labridae). Smithson. Contrib. Zool. 254, 27 p.

BIOLOGY OF THE WHITEBONE PORGY, *CALAMUS LEUCOSTEUS*, IN THE SOUTH ATLANTIC BIGHT[1]

C. WAYNE WALTZ, WILLIAM A. ROUMILLAT, AND CHARLES A. WENNER[2]

ABSTRACT

Whitebone porgy, *Calamus leucosteus*, were taken in trawl surveys over reef and nonreef habitats in the South Atlantic Bight in depths of 11 to 88 m. Larger individuals were taken in greater depths. Twelve age groups can be identified with sectioned otoliths and nine using scales. Annulus formation for otoliths and scales occurs between June and July. Von Bertalanffy growth equations of $L_t = 331\left[1 - e^{-0.1731\,(t+2.6390)}\right]$ from otoliths and $L_t = 362\left[1 - e^{-0.2611\,(t+0.3973)}\right]$ from scales suggest that attainment of maximum size for this species is similar to reports for other reef species. The fork length-weight relationship for *C. leucosteus* can be described by $W = 0.00004\ \mathrm{FL}^{2.907}$. The whitebone porgy is a protogynous hermaphrodite; younger, smaller fish are predominately females, and older, large fish are mostly males. Sexual transition most commonly occurs between ages II-IV and fork lengths 18-25 cm. Peak spawning occurs in May with total fecundity ranging from 30,400 to 1,587,400 eggs. The fecundity-weight relationship can be described by $F = 10.29438\ W^{1.6562}$. Regional landings data are not available for *C. leucosteus*; however, it was the third and fourth most abundant species by weight from trawler landings in South Carolina during 1979 and 1980.

The whitebone porgy, *Calamus leucosteus*, occurs from the Carolinas south to the Florida keys and throughout the Gulf of Mexico (Fischer 1978). Although more abundant and more frequently encountered in or near sponge-coral habitats at depths from 10 to 100 m (Fischer 1978; Powles and Barans 1980), individuals are sometimes taken from predominantly sandy bottoms (Wenner et al. 1979). This species is of commercial importance to trawl fishermen, but little information is available on its life history. The purpose of this paper is to present data on age, growth, reproductive biology, distribution, and relative abundance of *C. leucosteus* in the South Atlantic Bight.

MATERIALS AND METHODS

Distribution and relative abundance were determined from seasonal (fall 1973 to winter 1977) stratified random otter trawl surveys (Grosslein 1969) from Cape Fear, N.C., to Cape Canaveral, Fla. Sampling was conducted from the RV *Dolphin* with a 3/4 scale version of a Yankee No. 36 otter trawl (Wilk and Silverman 1976) towed for 0.5 h at 6.5 km/h.

Most specimens (~98%) used for analysis of age, growth, and reproductive biology were collected with otter trawls (3/4 Yankee No. 36, 40/54 fly net, University of Rhode Island high rise trawl (Hillier 1974)) from 1975 to 1980. The remainder were caught with baited fish traps and handlines. Fish were weighed (nearest gram) and measured (nearest mm total length [TL], fork length [FL], and standard length [SL]). Sagittae and scales from beneath and/or just behind the posterior edge of the pectoral fin below the lateral line were removed and stored dry. Impressions of several scales from each fish were made on clear acetate sheets with a model C Carver Laboratory Press[3] (1,547-1,687 kg/cm², 65.5°C, 5-10 min). Readability was reduced in large otoliths due to clouding of the central area and crowding of the rings along the outer margin; opaqueness also increased in all otoliths with storage time. These problems were corrected by preparing dorsal-ventral cross sections (~0.4 mm thick) on a plane perpendicular to the anterior-posterior axis through the center of the nucleus with a Buehler Isomet low speed saw.

Aging structures were analyzed using transmitted light on a microprojector at 40×. Scale measurements were made on a line through the center of the scale from the focus to the outer edge, whereas otolith measurements were taken from the center of the nucleus to the outer

---

[1] MARMAP Contribution No. 190 and Contribution No. 141 of the South Carolina Marine Resources Research Institute.

[2] South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted February 1982.
FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

margin along the ventral edge of the sulcus acousticus. Two independent readings were made on each.

Most analyses were performed using the Statistical Analysis System (Helwig and Council 1979). A FORTRAN program based on Poole (1961) gave back-calculated length at age. The von Bertalanffy growth equation (Bertalanffy 1938) was fitted to mean back-calculated fork length at age using parameters derived from Walford lines obtained by least square linear regressions (Everhart et al. 1975). All regression equations other than the regressions of radial measurement on fork length are the functional regressions of Ricker (1973, 1975).

Sex and reproductive condition of most fish were determined by histological examination of the gonads, which were fixed in formal-alcohol solution (Humason 1972). Tissues were prepared for embedding by passage through an Autotechnicon Duo Model 2A Automatic Tissue Processor. Gonads were embedded in paraffin, sectioned at $\sim 7\mu$ with a rotary microtome, stained with Harris' hematoxylin and counterstained with eosin Y. The first 200 slides were read by two individuals, then, following agreement on interpretation, the remaining sections were viewed by a single observer. Sex and maturity codes were formed by modifying Moe (1969) and Mercer (1978) and applying the four part index of Hilge (1977). The sex codes include hermaphrodite recognition and, when used with the maturity stages, give an accurate and objective estimate of reproductive status. Sexes were identified as undifferentiated, male, female, simultaneous hermaphrodites, male-predominating hermaphrodite, and female-predominating hermaphrodite. Maturity was classed as follows:

Class	*Testicular state*	*Ovarian state*
Immature	little or no spermatocyte development	small, basophilic oocytes
Ripening	from gonads with a few primary and secondary spermatocytes through those where lumen filled with spermatozoa	from relatively acidophilic oocytes through large yolky oocytes
Ripe (running)	predominance of spermatozoa, little active spermatogenesis	predominance of yolk filled oocytes, few hydrated eggs present
Spent	no spermatogenic activity, some residual sperm present in tubules	nonspawned mature eggs becoming atretic
Resting	some mitotic regeneration of spermatogonia	predominately with small basophilic oocytes, few traces of atretic activity
Transitional	resting testicular tissue with ovarian tissue in active development	resting ovarian tissue with testicular tissue in active development.

Terminology used in histological descriptions of gonadal development follows Hyder (1969) and Combs (1969).

Fecundity estimates were obtained from developing ovaries which were weighed (nearest gram) and placed in Gilson's solution (Humason 1972). Following digestion of the connective tissue and external tunic, the eggs were washed and stored in 50% isopropyl alcohol. Eggs were diluted to 1 l, and three to four 1 ml subsamples were removed from a well-mixed suspension, placed in gridded petri dishes, and counted at 12×. The mean of the individual counts expanded to the 1 l volume was used to estimate total fecundity. Histological examination revealed that eggs of diameter <0.15 mm were retained in spent ovaries without signs of atresia, while larger unshed oocytes atrophied. Eggs >0.15 mm were considered potential gametes for the impending spawn and were the only ones included in the fecundity estimates.

RESULTS

Distribution and Abundance

Calamus leucosteus occurred in 94 of 575 stratified random otter trawl tows in depths <110 m during research survey cruises from 1973 to 1977. This species was taken in depths of 11 to 88 m from lat. 28 °50′N to 34°36′N (Fig. 1). Although whitebone porgies were caught over the sandy bottom of the open shelf habitat, they were more frequently taken in trawl tows that contained sponges and corals, indicative of isolated patch reefs. *Calamus leucosteus* was found in 58% of the 67 trawl tows containing live bottom organisms and 11% of the open shelf tows during the surveys from 1973 to 1977. During the spring of 1978, otter trawl sampling in shallow water (18-42 m) sponge-coral habitat from Florida to North Carolina collected *C. leucosteus* in 43 of 57 tows. Thus, *C. leucosteus* may be found in reef and nonreef habitats in the South Atlantic Bight.

Seasonal catch/tow values indicated that *C. leucosteus* moved into warmer offshore waters

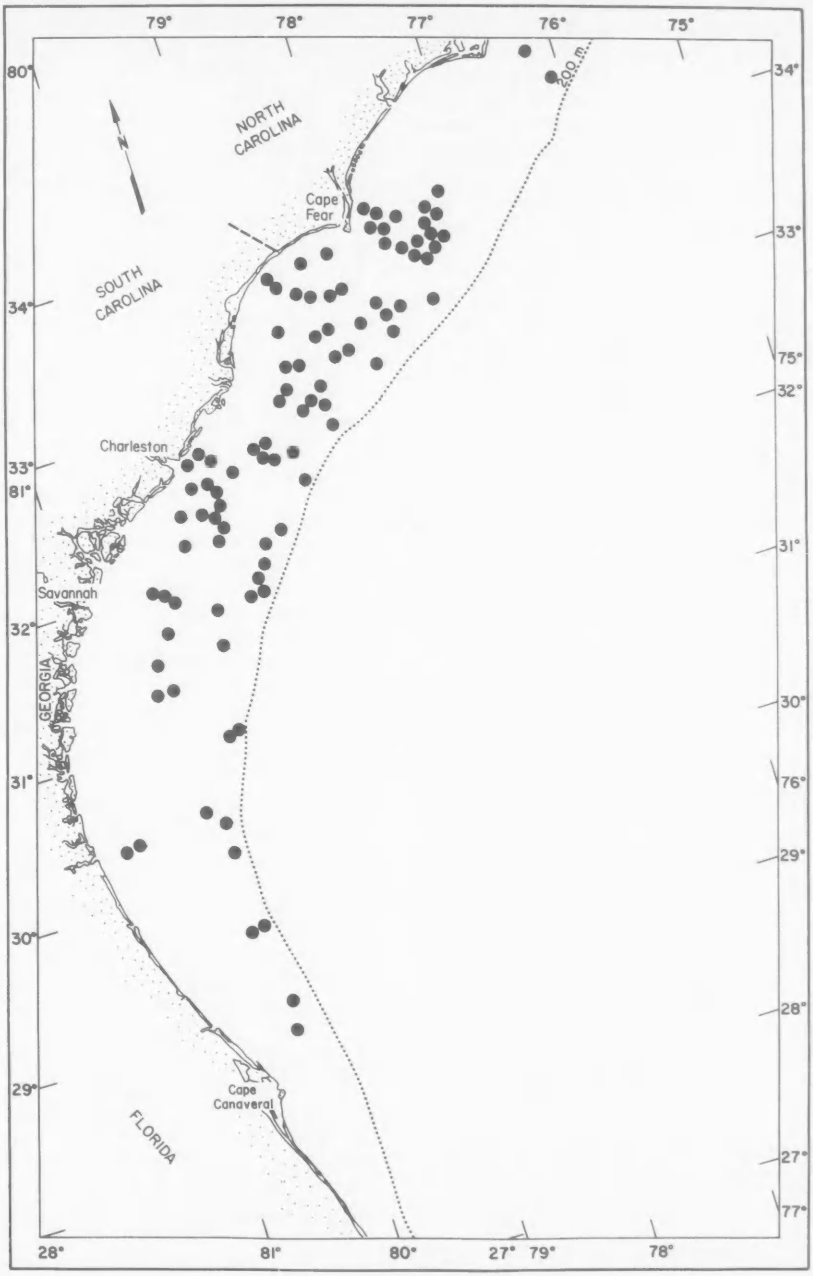

79°
78°
77°
76°
75°
80°
34°
200 m
NORTH CAROLINA
N
Cape Fear
33°
SOUTH CAROLINA
34°
75°
32°
Charleston
33°
81°
31°
Savannah
32°
GEORGIA
30°
31°
76°
29°
30°
28°
29°
Cape Canaveral
FLORIDA
27°
77°
28°
81°
80°
27°
79°
78°

FIGURE 1.—Locations where whitebone porgy, *Calamus leucosteus*, were taken during stratified random trawl surveys from 1973 to 1977.

during winter months, when inshore waters of the South Atlantic Bight have their annual minimum values (Table 1). They were absent in 55 trawl tows made during winter in the 9-18 m depth zone and showed variable frequencies of occurrence in other seasons in comparable depths.

A trend for an increase in modal length with increasing trawl depth was apparent (Fig. 2). All specimens <24 cm FL were encountered in depths <56 m.

TABLE 1.—Catch/tow values from whitebone porgies, *Calamus leucosteus*, from stratified random research surveys from 1973 to 1977. n_1 = number of trawl tows which contained *C. leucosteus*; n = total trawls in depth zone.

Season	Catch/tow	Depth zone (m)			
		9-18	19-27	28-55	56-110
Winter	$\bar{x}$ catch/tow number	0	4.0	2.0	0.7
	$\bar{x}$ catch/tow weight (kg)	0	1.23	1.07	0.43
	n_1/n	0/55	13/50	9/66	4/42
Spring	$\bar{x}$ catch/tow number	0.3	1.4	0.3	1.3
	$\bar{x}$ catch/tow weight (kg)	0.03	0.55	0.10	1.03
	n_1/n	2/22	5/20	4/28	4/18
Summer	$\bar{x}$ catch/tow number	4.3	2.6	3.1	0.6
	$\bar{x}$ catch/tow weight (kg)	1.12	1.02	1.65	0.43
	n_1/n	9/48	10/50	16/66	5/41
Fall	$\bar{x}$ catch/tow number	2.7	2.6	0.8	0.6
	$\bar{x}$ catch/tow weight (kg)	0.82	1.08	0.24	0.52
	n_1/n	4/18	4/18	3/19	2/14

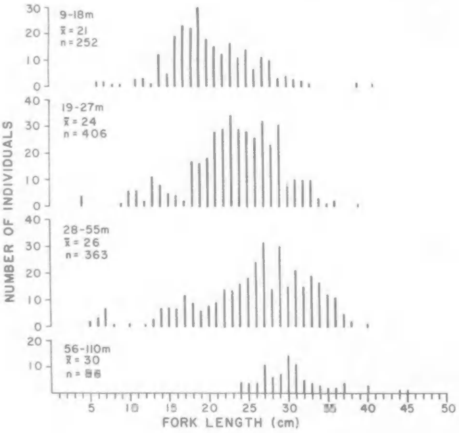


FIGURE 2.—Length-frequency distribution of *Calamus leucosteus* by depth zone for 3/4 Yankee trawl caught specimens (1973-77).

Age and Growth

Life history information was obtained from 1,732 fish collected from 1975 to 1980. Age determinations were attempted for 1,664 pairs of otoliths and 1,679 scale samples, and of these, 80% of the otoliths and 45% of the scales showed discernible rings. There was a 62.8% 1:1 agreement in ages obtained from both scales and otoliths from 760 individuals.

Mean marginal increments by month for scales and otoliths were examined to determine the time of annulus formation (Fig. 3). Samples were combined by month regardless of the year of capture. Mean marginal increments should approach zero at the time of annulus formation; this occurs in June on scales and in July on otoliths.

Fork lengths increased with increasing age as shown by scales and otoliths (Table 2); however, this progression was obscured in older age groups by smaller sample sizes. In general, average fork lengths derived from scale age and otolith age were similar for the first few years, then fish aged by otoliths tended to be smaller then those aged by scales. Fish given identical ages using both scales and otoliths showed average fork lengths at age similar to those derived by scales alone.

The relationships of fork length to otolith and scale radius were best described by the equations

$$\log FL = 1.041 + 0.844 \log OR$$
$$n = 1{,}320 \quad r^2 = 0.70$$

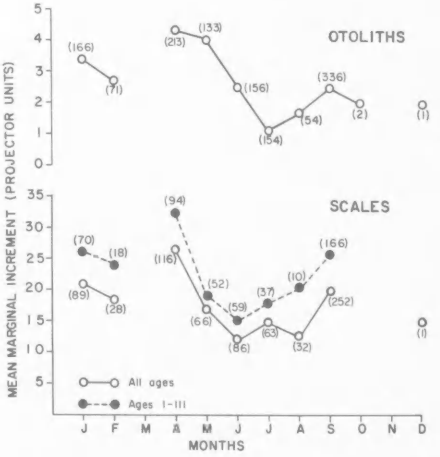


FIGURE 3.—Mean marginal increments for otoliths and scales by month for *Calamus leucosteus*. Number in parentheses = sample size.

TABLE 2.—Mean observed fork length, number and standard deviation (SD) by age for otoliths, scales, and individuals given identical ages by scales and otoliths of *Calamus leucosteus*.

	Otoliths			Scales			Otolith-scales		
Age	No.	$\overline{FL}$	SD	No.	$\overline{FL}$	SD	No.	$\overline{FL}$	SD
0	34	111	22.4	24	98	18.2	16	96	17.9
I	174	153	25.6	122	143	23.4	98	144	22.6
II	319	201	23.5	238	191	22.1	183	194	20.5
III	172	225	23.2	145	225	22.0	93	225	20.1
IV	138	248	22.5	73	256	28.9	41	247	20.0
V	155	263	26.3	77	284	30.8	29	280	27.7
VI	109	280	27.2	54	314	29.0	10	314	19.9
VII	73	284	31.6	18	312	33.5	6	295	44.0
VIII	57	279	32.0	6	345	29.3	—	—	—
IX	34	289	26.1	2	313	66.4	—	—	—
X	25	290	31.5	—	—	—	—	—	—
XI	26	301	33.0	—	—	—	—	—	—
XII	8	309	26.9	—	—	—	—	—	—

$$FL = -36.713 + 1.176\,SR$$
$$n = 757 \quad r^2 = 0.82$$

where FL = fork length (mm), OR = otolith radius (projector units), and SR = scale radius (projector units). The intercepts of these predictive equations were used as correction factors in deriving average back-calculated fork length at age (Table 3). Average back-calculated fork lengths for fish aged with otoliths up to age XII are 136, 179, 207, 227, 242, 252, 259, 264, 273, 280, 291, and 301 mm. For fish aged with scales up to age IX average back-calculated fork lengths were 102, 170, 215, 249, 275, 298, 303, 323, and 306 mm. Average observed fork lengths were greater than average calculated lengths in all cases for otolith and scale ages. Calculated lengths for fish aged with otoliths show a closer agreement with observed lengths than do calculated lengths derived using scales.

Mean back-calculated fork lengths (otolith ages: I-XII; scale ages: I-VIII) were used to obtain von Bertalanffy growth equations. Trial values of $L_\infty = 304$ for otoliths and $L_\infty = 349$ for scales appeared low. We were able to determine the best value of L_∞ by using several trial values of L_∞ and regressing $\ln(L_\infty - L)$ against t, where L = mean back-calculated fork length and t = age (Ricker 1975). The straightness of this line is sensitive to changes in L_∞ and the L_∞ that produced the straightest line was $L_\infty = 331$ for otoliths and $L_\infty = 362$ for scales. Values of $K = 0.1731$, $t_0 = -2.6390$ for otolith ages and $K = 0.2611$, $t_0 = -0.3973$ for scale ages were obtained. The theoretical growth equations derived from these values were

$$\text{otoliths } L_t = 331 \left[1 - e^{-0.1731(t+2.6390)}\right]$$
$$\text{scales } L_t = 362 \left[1 - e^{-0.2611(t+0.3973)}\right].$$

Theoretical, back-calculated, and observed fork lengths at age for scales and otoliths are compared in Figure 4.

TABLE 3.—Back-calculated fork length at age for *Calamus leucosteus* aged by scales and otoliths.

	Otoliths				Scales			
Age	No.	$\overline{FL}$	SD	Range	No.	$\overline{FL}$	SD	Range
I	1,286	136	17.3	54-231	733	102	20.0	31-183
II	1,112	179	19.3	101-269	611	170	22.9	92-238
III	793	207	21.5	110-273	373	215	26.3	116-297
IV	621	227	23.7	152-303	228	249	28.9	164-334
V	483	242	26.5	165-325	155	275	30.2	189-345
VI	329	252	28.4	180-339	79	298	30.1	200-363
VII	222	259	29.0	186-347	25	303	33.0	238-352
VIII	150	264	28.3	193-360	7	323	42.0	244-366
IX	93	273	28.4	199-354	2	306	63.9	261-351
X	59	280	29.7	209-350	—	—	—	—
XI	34	291	31.3	245-370	—	—	—	—
XII	8	301	24.9	272-340	—	—	—	—

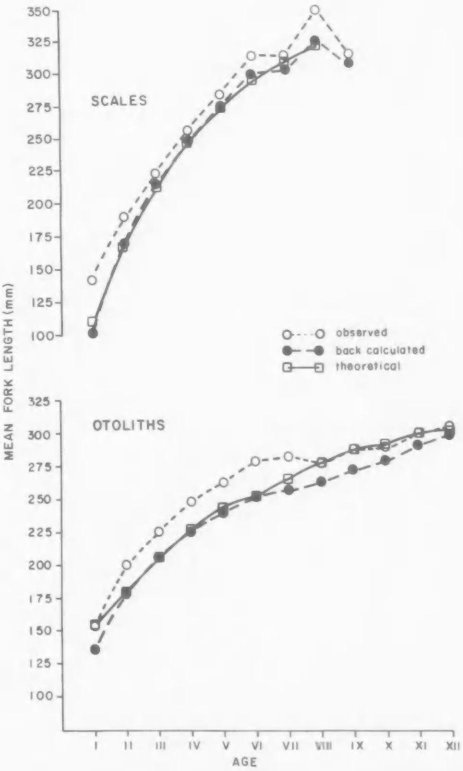


FIGURE 4.—Observed, back-calculated, and theoretical fork lengths of *Calamus leucosteus* aged by scales and otoliths.

Functional length-length and length-weight relationships for *C. leucosteus* are (length in millimeters; weight in grams)

$$FL = 1.13(SL) + 3.9 \quad n = 1464 \quad r^2 = 0.97$$
$$FL = 0.86(TL) - 2.0 \quad n = 1428 \quad r^2 = 0.98$$

$$\log Wt = 2.907(\log FL) - 4.367 \quad n = 1{,}719 \quad r^2 = 0.97$$
$$\log Wt = 2.858(\log SL) - 4.078 \quad n = 1{,}454 \quad r^2 = 0.98$$
$$\log Wt = 2.903(\log TL) - 4.553 \quad n = 1{,}416 \quad r^2 = 0.97.$$

Reproduction

Male and female gonads of *Calamus leucosteus* are paired glands suspended in the posterior body cavity by mesorchia. They join posteriorly into a common duct before the external genital opening. Gonads must be examined histologically for determination of both sex and maturity. Many of the 1,274 fish examined showed protogyny.

Immature female gonads possessed only small ($<100\ \mu$), densely basophilic oocytes (Fig. 5A) whereas developing ovaries showed a predominance of larger ($\sim$100-500 μ) acidophilic oocytes (Fig. 5B). Paraffin infiltration was poor in large ($\sim$500-700 μ), hydrated oocytes and resulted in unsatisfactory sections of ripe ovaries. Atretic oocytes (Fig. 5C) were common in spent gonads whereas resting tissue was identified by traces of atresia and the predominance of small basophilic oocytes. Transitional gonads had most of their bulk as nonactive ovarian tissue, while the testicular tissue was developing (Fig. 5D).

The small, immature testes showed little spermatogenic activity and were largely composed of primary and secondary spermatogonia. Early spermatogenesis and all phases of sperm formation through packing of lumina with spermatozoa (Fig. 6A) were characteristic of developing testes. Ripe testes showed little spermatogenesis with all lumina filled with sperm. Spent testes had convoluted tubules with evidence of residual sperm resorption. The resorptive process was largely completed in resting testes, and mitotic proliferation of spermatogonia had started.

Residual oocytes were present in 58% of the males. These were treated as functional males and all maturity stages (except immature) given to normal males were applied to these primarily male hermaphrodites (Fig. 6B). Traces of nonactive testicular tissue were found in 16.2% of the females (Fig. 6C), and these were treated as functional females. Juvenile hermaphrodites and a few other specimens in which both types of gonadal tissue were not only present, but equally developed, were considered simultaneous hermaphrodites (Fig. 6D). This phenomenon occurred in 3.4% of all gonads and was excluded from further analysis.

Females (Fig. 7) accounted for about 80% of the smaller, younger fishes, while males comprised approximately 70% of the largest size groups and about 80% of the oldest fish. Fish undergoing transition were found in ages I through VII (Fig. 7) and clustered around inflection points of both graphs (lengths: 18-25 cm FL; ages: II-IV). These figures imply that about 20% of young males remain males throughout life and that approximately 20% of the females remain females. Histological evidence demonstrates no case of males transforming to females and indicates females occur in all size and age groups sampled. Thus, approximately 60% of *C. leucosteus* undergo sex reversal.

This species spawns from April to August with peak spawning probably in May (Table 4). Of the fish examined, 100% were developing in March;

TABLE 4.—Percentages of *Calamus leucosteus* in different gonadal states by month of capture.

Month	*n*	Immature	Developing	Ripe	Spent	Resting	Transitional
January	117	2.0	42.4	—	1.0	55.6	—
February	84	—	31.0	—	25.2	41.0	3.6
March	16	—	100.0	—	—	—	—
April	238	11.9	79.1	8.1	1.0	1.0	0.5
May	157	6.4	41.5	32.3	16.0	4.5	—
June	162	17.3	42.1	2.6	14.2	19.8	3.7
July	173	15.6	18.7	3.6	9.9	50.3	—
August	60	1.7	31.7	3.4	1.7	46.7	11.7
September	214	12.7	27.6	—	1.9	44.0	13.6
October	2	—	—	—	—	100.0	—
November	—	—	—	—	—	—	—
December	1	—	—	—	—	100.0	—

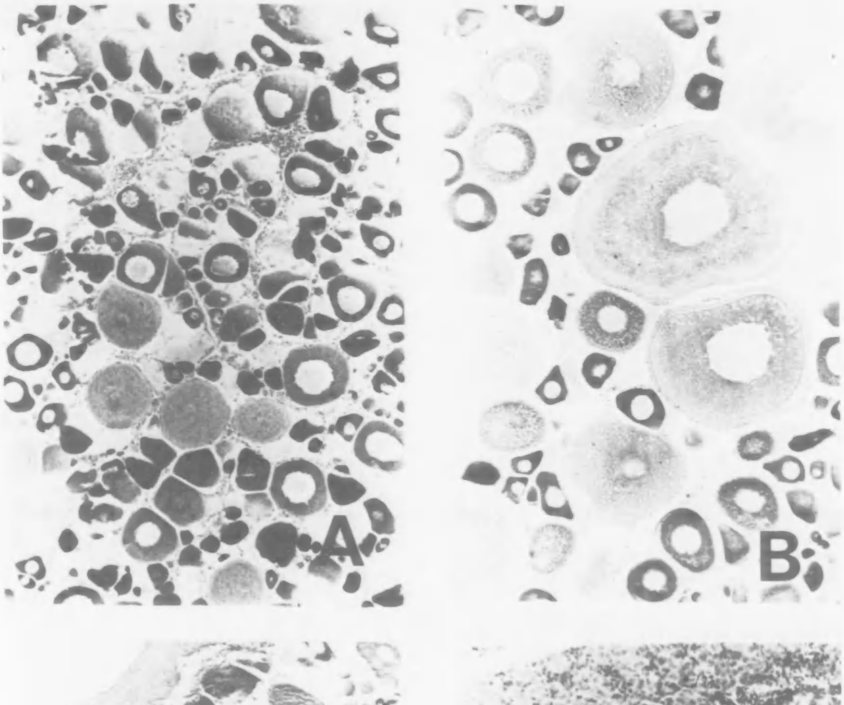


FIGURE 5.—Histological sections of *Calamus leucosteus* gonads. A, immature female; B, developing female; C, spent female; D, transitional gonad. AT = atretic oocyte, T = testicular tissue.

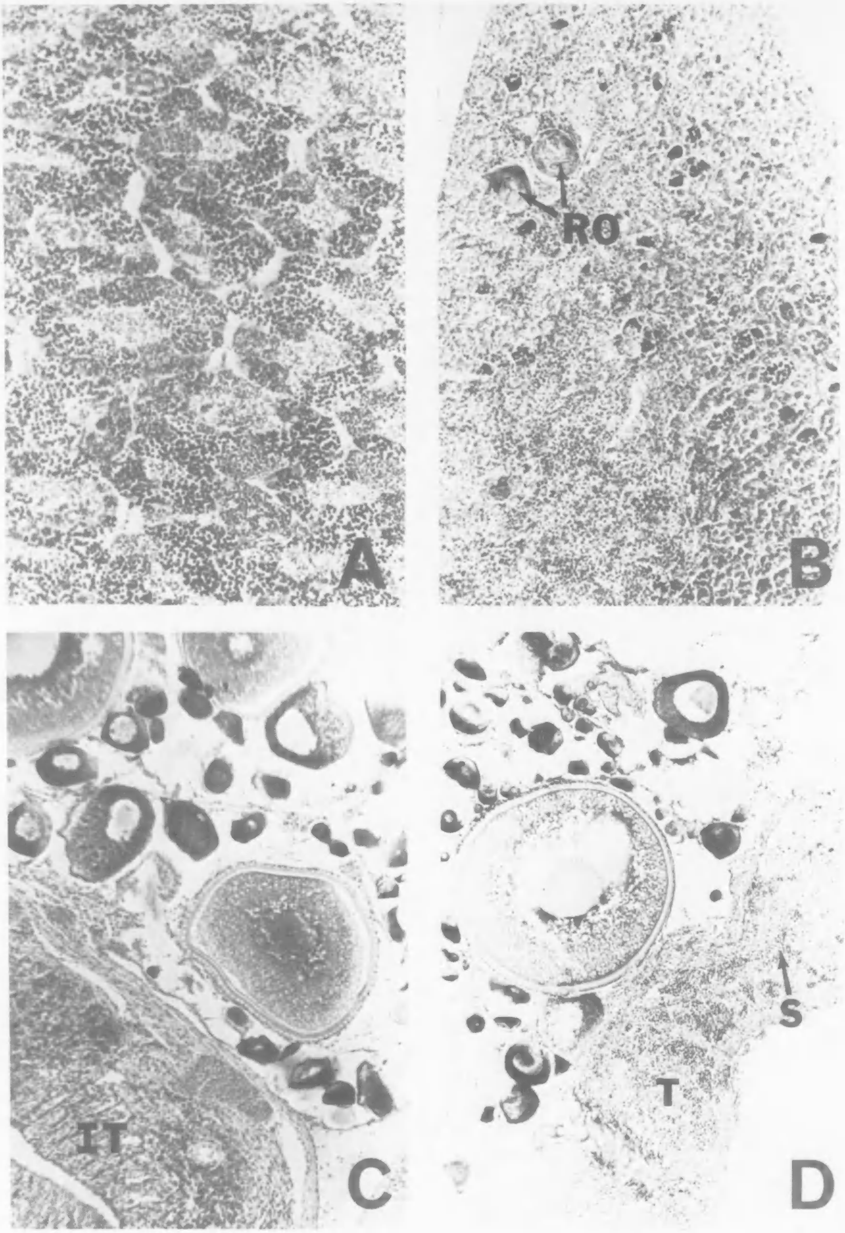


FIGURE 6.—Histological sections of *Calamus leucosteus* gonads. A, developing male; B, developing male with residual oocytes in testes; C, developing female with inactive testicular tissue present; D, simultaneous development in both ovarian and testicular tissue. IT = inactive testicular tissue, RO = residual oocyte, S = spermatozoa, T = testicular tissue.

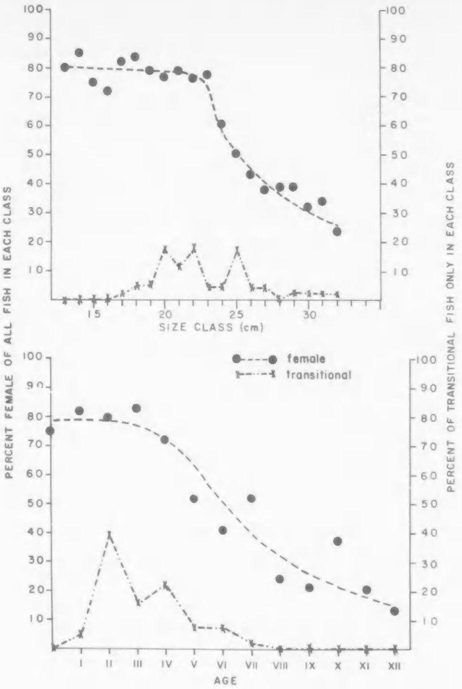


FIGURE 7.—Percent of all *Calamus leucosteus* that were females or functional females and the percent occurrence of transitional fish only by size and age.

this decreased to 79% in April, whereas the highest percentage of ripe fish were observed in May (32%). No ripe fish were encountered before April or after August. Fish undergoing transition were more frequently encountered after spawning (Table 4). The highest percentages of transitional fish were observed in August (11.7%) and September (13.6%). Both sexes may mature at age 1 and females as small as 179 mm FL have been observed with hydrated eggs.

Fecundity ranged from 30,400 to 1,587,400 eggs and generally increased with age (Table 5). It was significantly related to length and weight. The functional regressions for fecundity verses length and weight are

$$\log \text{fecundity} = 4.463(\log FL) - 5.347$$
$$n = 63 \quad r^2 = 0.64$$
$$\log \text{fecundity} = 4.475(\log SL) - 5.093$$
$$n = 63 \quad r^2 = 0.66$$

TABLE 5.—Otolith age-mean fecundity values for *Calamus leucosteus*. The Bliss (1967) approximation was used in transforming the mean from logarithmic to arithmetic units.

Age	Number of individuals	Mean fecundity	Range
I	3	85,192	59,000-129,400
II	11	124,911	30,400-334,700
III	16	215,601	63,700-366,700
IV	5	236,892	119,400-431,400
V	9	285,824	145,000-532,400
VI	4	236,674	60,400-374,700
VII	6	266,348	174,000-617,700
VIII	—	—	—
IX	—	—	—
X	1	869,400	—
XI	1	1,587,400	—

$$\log \text{fecundity} = 4.501(\log TL) - 5.742$$
$$n = 62 \quad r^2 = 0.64$$
$$\log \text{fecundity} = 1.656(\log W) + 1.013$$
$$n = 63 \quad r^2 = 0.66$$

where *FL*, *SL*, and *TL* are in mm and *W* in g.

South Carolina Commercial Landings

Regional catch and landing data for *C. leucosteus* are available only as the combined values of *C. leucosteus* and *Stenotomus* sp. from the offshore trawl fishery (Table 6). Whitebone porgy represent approximately 98% of these values (Ulrich[4]). The mean size of random subsamples of the trawl catch (1979: $\overline{FL} = 27$ cm; 1980: $\overline{FL} = 26$ cm) was very similar for both years (Fig. 8).

TABLE 6.—Reported landings of *Calamus leucosteus* and *Stenotomus* sp. from the South Carolina offshore trawl fishery 1979 and 1980. Values for November and December 1980 are low because of incomplete landings data from one Charleston, S.C. dock.

	1979		1980	
Month	Weight (kg)	Percent of total catch	Weight (kg)	Percent of total catch
January	1,525	20	4,794	11
February	3,452	18	4,178	9
March	2,722	12	5,081	7
April	2,779	12	3,346	9
May	264	3	560	6
June	132	11	n.a.[1]	—
July	n.a.	—	n.a.	—
August	n.a.	—	n.a.	—
September	n.a.	—	n.a.	—
October	n.a.	—	n.a.	—
November	n.a.	—	2,180	16
December	n.a.	—	1,536	12
Total	10,873	13.4	21,675	9.2

[1] n.a. = not available.

---

[4] G. Ulrich, Finfish Management Section, Division of Marine Resources, South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412, pers. commun. 19 May 1980.

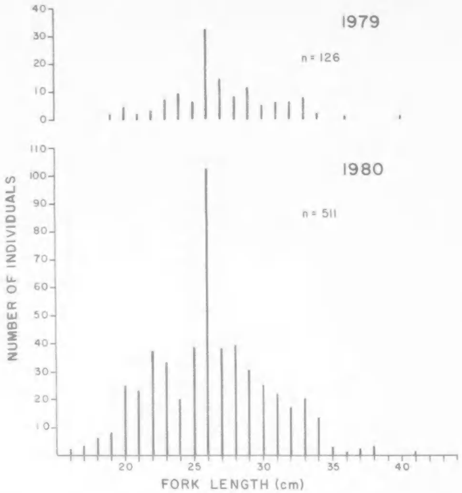


FIGURE 8.—Length-frequency subsamples from trawl caught *Calamus leucosteus* landed in South Carolina offshore trawl fishery, 1979 and 1980.

DISCUSSION

The time of annulus formation is similar in otoliths and scales, it occurs when water temperatures are warm, photoperiod is long, and, in mature fish, just after spawining. The annulus is formed later in the year (June-July) than in some other reef species: vermilion snapper, *Rhomboplites aurorubens*, March-May (Grimes 1978); black sea bass, *Centropristis striata*, March-June (Mercer 1978); red porgy, *Pagrus pagrus*, March-April (Manooch and Huntsman 1977).

Twelve age groups could be identified using otoliths, whereas only nine were determined from scales because of the inability to read those of older fish. In addition, some older fish aged with otoliths had one or more rings than scales. As a result, larger fish aged by scales appear younger than those aged by otoliths, and this is reflected in back-calculated and theoretical lengths at age. The relationship of fork length to otolith radius appears to be curvilinear. The measurement of otolith radius used in this study is actually a measurement of otolith thickness. Beamish (1979) noted in the Pacific hake, *Merluccius productus*, that growth of all parts of the otolith was not identical throughout the life of the fish. He found that growth of older otoliths continues, but that increases in thickness, especially in the ventral interior portion, becomes proportionally more important than increases in otolith length or height. *Calamus leucosteus* appears to be best aged, using this measurement from sectioned otoliths.

Estimates of $L_\infty = 331$ mm FL for otoliths and 362 mm FL for scales appear low since a maximum size of 18 in TL (391 mm FL) was reported by Jordan and Gilbert (1884) and we observed a 407 mm FL fish. The calculation of L_∞ depends on the number of age groups present and the distribution of individuals within each group. Higher values of L_∞ should have been expected if a larger number of bigger older fish could have been aged and included in the calculations. Comparison of growth coefficients (scales: $K = 0.2611$; otoliths: $K = 0.1731$) indicates that *C. leucosteus* attains maximum size at a rate similar to *Centropristis striata*, $K = 0.219$ (Mercer 1978), *Pagrus pagrus*, $K = 0.096$ (Manooch and Huntsman 1977), *Rhomboplites aurorubens*, $K = 0.198$ (Grimes 1978), and red grouper, *Epinephelus morio*, $K = 0.179$ (Moe 1969).

Calamus leucosteus spawns from April through August, with peak spawning in May. Both sexes may mature at age 1 and fecundity estimates range from 30,400 to 1,587,400 eggs. *Pagrus pagrus*, another commercially important sparid occupying the same range, spawns from January through April, matures at age 2, and has fecundity estimates ranging from 48,660 to 488,600 eggs (Manooch 1976).

Calamus leucosteus, as well as several western Atlantic sparids (Reinboth 1970; Manooch 1976; Roumillat pers. obs.), demonstrates protogynous hermaphroditism, which can only be determined by histological observations. Sexual transition in *C. leucosteus* involves the rapid proliferation of testicular tissue in the posteroventral tunica of the ovary which is the typical sparid protogynous pattern (Smith 1975). The testes does not infiltrate the ovarian lamellae as in groupers (Smith 1965), but envelops the regressing female tissue. Male and female tissues are separated during transition by connective tissue, but the sperm ducts pass within the ovarian wall. Other western Atlantic families that demonstrate protogynous hermaphroditism in addition to the Sparidae are the Serranidae (Smith 1965, 1975), the Labridae (Warner and Robertson 1978), and Scaridae (Robertson and Warner 1978). The labrids and scarids have complex socially influenced reproductive strategies that have not yet been documented for sparids or serranids.

The South Carolina offshore trawl fishery is highly seasonal. Landings are greatest during the winter months after the closing of the shrimp season. *Calamus leucosteus* is the third or fourth most abundant species by weight in trawler landings. These are primarily age IV-VI fish. Red porgy and vermilion snapper are the most abundant trawl-caught commercial fish.

ACKNOWLEDGMENTS

We thank all MARMAP field personnel, Captain J. V. Causby, and the crew of the RV *Dolphin* for aid in specimen collection. D. Stubbs and P. K. Ashe processed, mounted, and stained gonadal tissue. G. Ulrich and D. Oakley provided catch statistics and commercial length-frequency samples. A. G. Gash, N. Kopacka, and D. Machowski aided in data processing techniques. K. Swanson drew the figures. M. Maddox (College of Charleston) helped with photomicrographs and B. J. Ashby typed the manuscript. V. G. Burrell, Jr. and R. A. Low reviewed the manuscript. This work is a result of research sponsored by the National Marine Fisheries Service (MARMAP Program Office) under Contract 6-35147 and by the South Carolina Wildlife and Marine Resources Department.

LITERATURE CITED

BEAMISH, R. J.
1979. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. J. Fish. Res. Board Can. 36:141-151.
BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth. (Inquiries on growth laws. II.) Hum. Biol. 10:181-213.
BLISS, C. I.
1967. Statistics in biology. Statistical methods for research in the natural sciences, Vol. 1. McGraw-Hill, N.Y., 558 p.
COMBS, R. M.
1969. Embryogenesis, histology and organology of the ovary of *Brevoortia patronus*. Gulf Res. Rep. 2:333-434.
EVERHART, W. H., A. W. EIPPER, AND W. D. YOUNGS.
1975. Principles of fishery science. Cornell Univ. Press, Lond., 288 p.
FISCHER, W. (editor).
1978. FAO species identification sheets for fishery purposes. Western Central Atlantic (fishing area 31). Food and Agricultural Organization of the United Nations, Rome, Vol. 5, pag. var.
GRIMES, C. B.
1978. Age, growth, and length-weight relationship of vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina waters. Trans. Am. Fish. Soc. 107:454-456.
GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.
HELWIG, J. T., AND K. A. COUNCIL (editors).
1979. SAS user's guide. 1979 ed. SAS Inst., Inc., N.C., 494 p.
HILGE, V.
1977. On the determination of the stages of gonad ripeness in female bony fishes. Meeresforschung 25(1976-1977):149-155.
HILLIER, A. J.
1974. URI high rise series bottom trawl manual. Univ. Rhode Island, Mar. Bull. 20, 6 p.
HUMASON, G. L.
1972. Animal tissue techniques. 3d ed. W. H. Freeman and Co., San Franc., Calif., 641 p.
HYDER, M.
1969. Histological studies on the testis of *Tilapia leucosticta* and other species of the genus *Tilapia* (Pisces: Teleostei). Trans. Am. Microsc. Soc. 88:211-231.
JORDAN, D. S., AND C. H. GILBERT.
1884. A review of the species of the genus *Calamus*. Proc. U.S. Natl. Mus. 7:14-24.
MANOOCH, C. S., III.
1976. Reproductive cycle, fecundity, and sex ratios of the red porgy, *Pagrus pagrus* (Pisces: Sparidae) in North Carolina. Fish. Bull., U.S. 74:775-781.
MANOOCH, C. S., III, AND G. R. HUNTSMAN.
1976. Age, growth, and mortality of the red porgy, *Pagrus pagrus*. Trans. Am. Fish. Soc. 106:26-33.
MERCER, L. P.
1978. The reproductive biology and population dynamics of black sea bass, *Centropristis striata*. Ph.D. Thesis, College of William and Mary, Williamsburg, Va., 211 p.
MOE, M. A., JR.
1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes), from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour. Mar. Res. Lab., Prof. Pap. 10, 95 p.
POOLE, J. C.
1961. Age and growth of the fluke in Great South Bay and their significance to the sport fishery. N.Y. Fish Game J. 8(1):1-18.
POWLES, H., AND C. A. BARANS.
1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. Mar. Fish. Rev. 42(5): 21-35.
REINBOTH, R.
1970. Intersexuality in fishes. Mem. Soc. Endocrinol. (Hormones and the Environment) 18:515-543.
RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 382 p.
ROBERTSON, D. R., and R. R. WARNER.
1978. Sexual patterns in the labroid fishes of the Western Caribbean, II: The parrotfishes (Scaridae). Smithson. Contrib. Zool. 255, 26 p.
SMITH, C. L.
1965. The patterns of sexuality and the classification of serranid fishes. Am. Mus. Novit. 2207, 20 p.
1975. The evolution of hermaphroditism in fishes. *In* R. Reinboth (editor), Intersexuality in the animal kingdom, p. 295-310. Springer-Verlag, N.Y.

WARNER, R. R., AND D. R. ROBERTSON.
1978. Sexual patterns in the labroid fishes of the western Caribbean, I: The wrasses (Labridae). Smithson. Contrib. Zool. 254, 27 p.

WENNER, C. A., C. A. BARANS, B. W. STENDER, AND F. H. BERRY.
1979. Results of MARMAP otter trawl investigations in the South Atlantic Bight. II. Spring, 1974. S.C. Mar. Resour. Cent. Tech. Rep. 40, 78 p.

WILK, S. J., AND M. J. SILVERMAN.
1976. Fish and hydrographic collections made by the research vessels *Dolphin* and *Delaware II* during 1968-72 from New York to Florida. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-697, 159 p.

OBSERVATIONS OF RIGHT WHALES, *EUBALAENA GLACIALIS*, IN CAPE COD WATERS[1]

WILLIAM A. WATKINS AND WILLIAM E. SCHEVILL[2]

ABSTRACT

Sightings of right whales, *Eubalaena glacialis*, in waters within 30 km of Cape Cod, Massachusetts, are reported for 1955-80. Aerial and shipboard observations indicate the occurrence of right whales in this area during most of the year. Sightings peaked during April and May. There were 641 sightings of individual right whales with 117 seen more than 1 day during a year (758 total sightings). Up to 165 whales were seen each year with a maximum 1-day sighting of more than 70 right whales. Behaviors and activities of these inshore whales are described. During the peak period these whales were often found feeding within 5 m of the surface. In other seasons the whales spent less time near the surface and were less visible. These observations do not represent a census because emphasis was placed on the study of the whales found and not on searching to find all the whales in the area.

Observations of northern right whales, *Eubalaena glacialis* Borowski 1781, made in nearshore waters of Cape Cod over a span of 25 yr are reported here, along with characteristic activities, groupings, and differences in visibility of these whales. These sightings (listed in Table 1 and in Schevill et al. 1981) indicated the occurrence of right whales in this area during most of the year and allowed repeated observations of their behavior. Although these sightings were not systematic enough to provide a census of the nearshore whales, they do indicate general patterns that complement more recent efforts to assess the right whale populations and distributions.

Right whales were found in large numbers in the Cape Cod area until about 1730 (Allen 1916), but this stock was systematically reduced by shore whaling that took all that could be caught, including cows and calves. Although heavy harvesting greatly reduced the population, right whales probably have never been totally absent from our waters, even though there seem to have been no published sightings between 1913 and 1955. A review of the historic data was given by Reeves et al. (1978) along with some recent observations.

Since 1955 we have recorded observations of these whales as encountered in Cape Cod waters. Attempts were made to assess their local occurrence, study their behavior, analyze their acoustic activity, and recognize individuals. We have described typical sounds (Schevill et al. 1962; Schevill and Watkins 1962), underwater activity extrapolated from recorded sounds (Watkins and Schevill 1971, 1972), feeding behavior (Watkins and Schevill 1976), and comparison of surface feeding activity with that of three other baleen whale species (Watkins and Schevill 1979).

METHODS

Right whales were observed in Cape Cod waters (Cape Cod Bay, Massachusetts Bay, Nantucket and Vineyard Sounds, Nantucket Shoals, and adjacent waters within about 30 km of the coast, roughly bounded by lat. 41°-43°N and long. 69°-72°W) both from the air and from the water, and occasionally at the same time. The whales were usually within 15 km of the beach, but sometimes were found 30 km or more from shore. Aerial observation allowed assessment of distinctive markings, size (by comparison with the shadow of the fuselage), and activity (feeding, social interaction, etc.). Surface observations from boats drifting quietly alongside the animals permitted photography, underwater sound recording, and behavioral observation. Sometimes contact could be maintained with the same individuals for up to 6 h. Most observations were in daylight, but some nighttime studies were made. In both aerial and shipboard work,

---

[1] Contribution No. 4642, Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

[2] Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

Manuscript accepted May 1982.

TABLE 1.—Summary of sightings of northern right whales, *Eubalaena glacialis*, (from Schevill et al. 1981). Repeaters (the same whales seen on more than 1 d during the year) have been subtracted from column D. Searches took place during all months, and there was equivalent search effort during the years 1959-66 and 1972-79. Roman numerals I through XII (Col. A) represent the months January through December.

	A	B	C	D	E	F
Year	Months in which whales were seen	No. days whales seen	Total no. whales seen	Total no. reduced by repeaters	Max. no. seen in one group	Max. no seen on 1 day
1955	I	1	2	2	2	2
1956	IV	4	24	6	6	6
1957						
1958	IV,V	2	9	9	6	6
1959	III,IV,VIII	16	73	51	7	30
1960	IV,V	6	76	61	16	21
1961	III,IV, V	18	165	131	8	32
1962	I,IV,V	5	15	15	6	6
1963	IV,V	2	5	5	2	4
1964	II,IV,V	8	50	50	4	17
1965	IV,V	6	21	20	3	5
1966	IV,V	5	25	25	4	8
1967						
1968						
1969						
1970	IV	1	70+	70+	30+	70+
1971						
1972	V	2	4	4	2	2
1973	III,IV,V	6	18	18	5	8
1974	IV,V	9	59	58	16	16
1975	I,II,III,IV,V,VI,VII	14	33	28	5	7
1976	III,IV,V,X	8	16	9	2	4
1977	III,IV,VIII,X	10	21	16	7	7
1978	III,IV,VII	10	39	39	9	9
1979	I,III,IV,V,VI	9	20	13	3	4
1980	II,IV,V	7	13	11	4	4
Total		149	758	641		

we customarily remained with the first whales that were found, staying with them as long as they could be studied.

Our searches for right whales were irregular, but were made in all months of the year as weather and other work permitted, mostly under conditions of light wind and good visibility. Fewer trips were made in winter because of poor weather and few sightings, increasing to one to five trips a week in spring with improved weather and greater abundance of whales, and then decreasing during summer and autumn as fewer whales were found. Usually, we made only one trip a day, by aircraft or boat. Sighting efficiency during searches was variable due to changes in weather and whale behavior. From the air, right whales feeding below surface often were located by the light reflected from their baleen. (Though dark above water, baleen appears pale when seen through the sea surface.) Individual whales sometimes were recognizable by natural skin marks and by the pattern of cephalic excrescences (often called callosities) variably covered by light-colored Cyamidae (Leung 1967), a method used for identifying Pacific right whales by Klumov (1962) and southern right whales, *Eubalaena australis*, by Payne (1974, 1976).

RESULTS

In 1955 we identified two right whales from an aerial photograph taken by Bruce M. Clark on 24 January in Cape Cod Bay off Barnstable, Mass. Then in 1956, six whales were found off Martha's Vineyard Island, south of Cape Cod. In 1958 we again found right whales in that area, and in Cape Cod Bay. Active searches began in 1959, and right whale sightings during 21 yr between 1955 and 1980 are summarized in Table 1 and listed in the article by Schevill et al. (1981). No searches were made in 1957 and in 1967-71, although a research cruise through the area in 1970 located a large group of right whales.

The same individual whales were ordinarily sighted for only a few days at a time. Although groups of whales often appeared and then disappeared together, the usual sequence was a procession of right whales through the area. Successive sightings several days apart and within the same area were often of different whales. Right whales were observed alone or in small groups of two to six adults (49% of the sightings), as cow-calf pairs, occasionally in larger aggregations, and in groups including adults and older calves. A wide variety of sizes was seen, from 5 m calves to adults of from 12 m to about 16 m. Calves were apparently born in these waters, since adults observed without calves sometimes were seen a short time later accompanied by small calves. We found no seasonality or geographic factor that could be related to group size. Sometimes new whales replaced individuals in groups seen on previous days.

During winter and early spring, right whales were difficult to observe because they were at the surface for relatively short periods and were easily disturbed. These whales sometimes blew underwater so that no surface blow (spout) was visible, and they did not always raise their flukes above water as they began a dive. In late spring, the whales were found feeding frequently at or near the surface (Watkins and Schevill 1976), and apparently were less disturbed by our presence. Thus, before the middle of April, sightings were usually short encounters, often sufficient only for identification. Later sightings generally were of more leisurely surfacings, allowing longer periods of observation.

Over the 21 yr there were 641 sightings of individual right whales, with 117 seen on more than 1 d during a year (758 total sightings including repeaters). Some whales were positively recognized as repeaters and others were suspected repeaters because of location, sizes, and markings. During the years 1959-66 and 1972-79, approximately equal time was spent on searches during corresponding seasons in likely sighting areas, although the number of whales and the months and number of days of whale sightings varied markedly (Table 1). The large number seen in 1970 was comprised of at least 30 whales close to our ship (for several hours) and two other large groups of at least 20 each a short distance away, totaling between 70 and 100 right whales. Most of our sightings have been in April (57%) and fewer in May (27%), although we usually have searched more than three times as much in May than in April because of improved weather.

In our usual search, the boat or aircraft first crossed Cape Cod Bay (1-5 times) before rounding Race Point and searching east and north of Cape Cod, and less often south of Martha's Vineyard and Nantucket Islands. Right whales were seen most often near the northern tip of Cape Cod (Race Point) where movement of water masses collects plankton in nearsurface concentrations (Watkins and Schevill 1976). Otherwise, the whales consistently did not seem to prefer locations within the search area. Right whales were sometimes seen a few hundred meters off the beach, but generally they were several kilometers from shore; thus their occurrence cannot be related to bottom topography. No habitual direction of movement was observed.

Few whales were recognized from one year to the next. Callosity patterns provided good separation of individuals within a small group of whales seen in one year, but often have not been distinctive enough for positive identification of animals from the larger population seen over several years. Many of the callosity patterns were similar, and because of the variability in light coloration (apparently caused mostly by movement of the cyamids), fine distinctions in the patterns have been difficult to separate. The callosity pattern on calves appeared to become more visibly distinct with age, perhaps as more cyamids occupied the growths. Comparison of aerial and boat views of the same callosity shapes shows that the nearly vertical aerial view (Fig. 1) loses small details because of distance, distortion through water, and relative density of cyamids, but it provides a good perspective of the pattern; whereas, the nearly horizontal view of the same whales from a boat (Fig. 2) provides good detail, but generally misses the overall shape.

The longest sequence of recognition of an individual right whale was that of a cow seen in 4 consecutive years, 1973-76. During the first and fourth years, this whale was accompanied by a very small calf. In 1974, the yearling calf still accompanied the cow, and in 1975 the cow was in a group that may have included this calf. In 1976, the cow with a new calf was seen repeatedly throughout 7 wk of observation. The pattern of callosities on this cow was very distinctive, but since 1976 a similar pattern has not been recognized.

Groups of right whales generally were involved in social as well as feeding activity. They sometimes broke off from feeding together to chase, splash, and roll against each other, often with three or more whales participating in sexual routines (penises sometimes visible).

The relative ease of sighting right whales depended on their activity at the surface. The respiration period was variable, often averaging 1 blow/min of dive cycle. Dive durations also

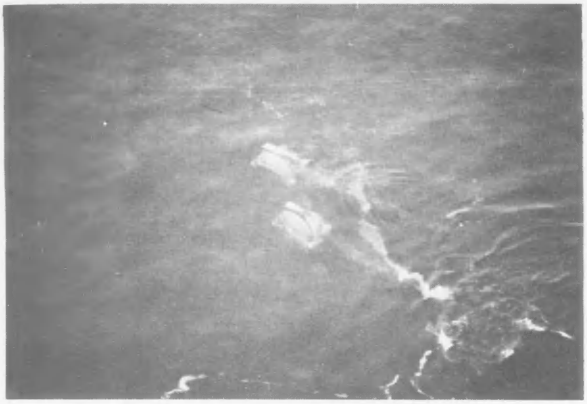


FIGURE 1.—Aerial view of two right whales feeding in a slick of collected plankton in Cape Cod Bay, Mass., 1 May 1979 (same individuals shown in Fig. 2). Note the pattern of head callosities and the pale appearance of the baleen underwater. Photo by K. E. Moore.

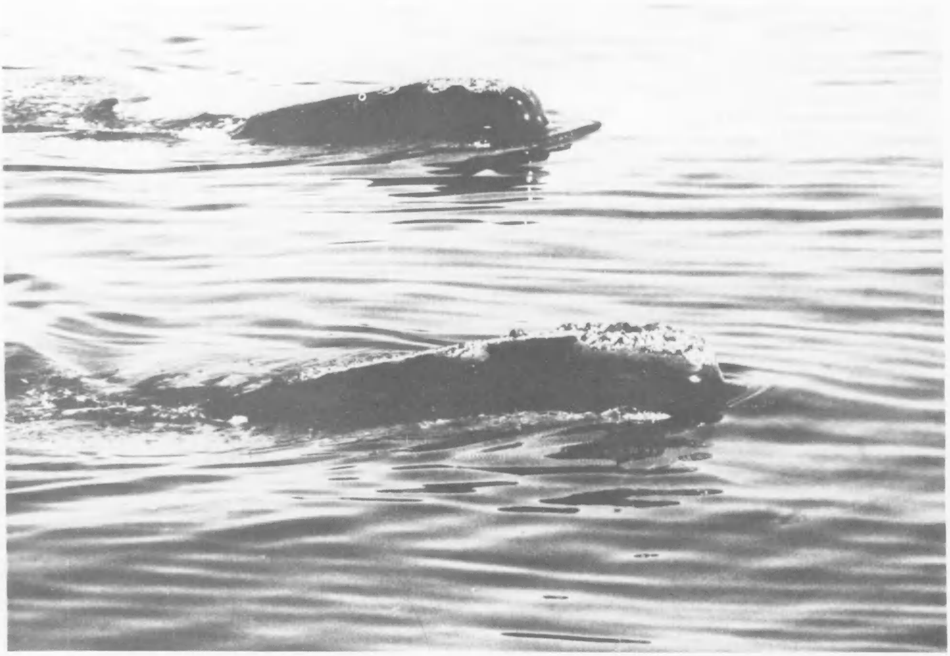


FIGURE 2.—View of two right whales seen from a boat in Cape Cod Bay, Mass., 2 May 1979 (same individuals as in Fig. 1). Note the limitation in visibility through the water surface, yet more visibility in details of head calosity patterns. These whales were observed for nearly 5 h as they fed nearby at the surface, but we found it difficult to record the complete callosity shape from these surface views. Photo by K. E. Moore.

varied from 1 to 7 min during feeding (Watkins and Schevill 1976), with occasional dives of 20 min or longer. Sometimes whales that had been conspicuous in their nearsurface activity suddenly changed their behavior to that of long dives and very little surface exposure.

During two observations of these whales in offshore waters, submergences of 20-22 min with nearsurface times of 10-12 min were recorded, demonstrating less surface activity than in the nearshore sightings. A group of 12 whales was observed at lat. 42°50′N, long. 65°00′W on 9 August 1974 and another group of 7 whales at lat. 42°51′N, long. 65°30′W on 2 August 1976 (not listed in Schevill et al. 1981). Both offshore groups were observed for more than 3 h, but very little surface activity was seen.

DISCUSSION

Our sightings do not provide a basis for a right whale census. Observations were sporadic and directed toward behavioral study, so that we usually remained with the first whales that were found. Although our efforts generally were confined to inshore waters, we note similar patterns reported in offshore surveys (Winn et al.[3]).

Variations in right whale surface behavior probably contribute to variability in sightings. In addition, the elusive behavior often noted in late winter and early spring, coupled with poor weather, may have been responsible for so few sightings during fall and early winter. The peak occurrence (April) of nearshore whales matches Allen's (1916) interpretation of the shore whaling data. He indicated that right whales were most abundant in the nearshore area during April and May, absent in July and August, and apparently abundant from November through March (the period of greatest catch).

The variability in the numbers of right whales sighted in 21 yr, the individual whales' apparent short stay in the area, the changing group compositions, and the few whales recognized from previous years all appear to indicate that we are seeing only a portion of a larger population of right whales. In other places and other seasons, they may not be as visible as they are during their stay in Cape Cod waters.

ACKNOWLEDGMENTS

We appreciate the help of a large number of observers who shared in the sightings of right whales over 25 yr: Robert G. Weeks, Stanley E. Poole, J. Bercaw, A. D. Colburn, and A. J. Avellar, as well as a host of others including Barbara Lawrence, Richard H. Backus, James E. Craddock, Teresa A. Bray, and Karen E. Moore. Preparation of the figures and correlation of the record of sightings were done by Karen E. Moore. James G. Mead, John H. Prescott, Randall Reeves, and Steven K. Katona helpfully reviewed the manuscript. Funding is from the Oceanic Biology Program of the Office of Naval Research (Contract N00014-82-C0019 NR 083-004).

LITERATURE CITED

ALLEN, G. M.
1916. The whalebone whales of New England. Mem. Boston Soc. Nat . Hist. 8(2), 322 p.

KLUMOV, S. K.
1962. The right whales in the Pacific Ocean. [In Russ., Engl. summ.] Tr. Inst. Okeanol. Akad. Nauk SSSR 58:202-297.

LEUNG, Y.-M.
1967. An illustrated key to the species of whale-lice (Amphipoda, Cyamidae), ectoparasites of Cetacea, with a guide to the literature. Crustaceana 12:279-291.

PAYNE, R.
1974. A playground for whales. Anim. Kingdom 77(2): 7-12.
1976. At home with right whales. Natl. Geogr. Mag. 149:322-339.

REEVES, R. R., J. G. MEAD, AND S. KATONA.
1978. The right whale, *Eubalaena glacialis*, in the western north Atlantic. Rep. Int. Whaling Comm. 28:303-312.

SCHEVILL, W. E., R. H. BACKUS, AND J. B. HERSEY.
1962. Sound production by marine animals. *In* M. N. Hill (editor), The sea, Vol. 1, p. 540-566. John Wiley and Sons, N.Y.

SCHEVILL, W. E., K. E. MOORE, AND W. A. WATKINS.
1981. Right whale, *Eubalaena*, *glacialis*, sightings in Cape Cod waters. Woods Hole Oceanogr. Inst., Tech. Rep. WHOI-81-50, 16 p.

SCHEVILL, W. E., AND W. A. WATKINS.
1962. Whale and porpoise voices. A phonograph record. Woods Hole Oceanogr. Inst., Woods Hole, Mass., 24-p. pamphlet and record.

WATKINS, W. A., AND W. E. SCHEVILL.
1971. Four hydrophone array for acoustic three-dimensional location. Woods Hole Oceanogr. Inst., Ref. No. 71-60, 33 p.
1972. Sound source location by arrival-times on a non-

---

[3] Winn, H. E., D. R. Goodale, M. A. M. Hyman, R. D. Kenney, C. A. Price, and G. P. Scott. 1981. Right whale sightings and the right whale minimum count. *In* A characterization of marine mammals and turtles in the mid- and north-Atlantic areas of the U.S. Outer Continental Shelf. Annual Report for 1979 Cetacean and Turtle Assessment Program, University of Rhode Island, Kingston, p. 1-37.

rigid three-dimensional hydrophone array. Deep-Sea Res. 19:691-706.

1976. Right whale feeding and baleen rattle. J. Mammal. 57:58-66.

1979. Aerial observation of feeding behavior in four baleen whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. J. Mammal. 60:155-163.

NOTES

FECUNDITY OF THE WIDOW ROCKFISH, *SEBASTES ENTOMELAS*, OFF THE COAST OF OREGON

During the past several years a strong fishery has developed for the widow rockfish, *Sebastes entomelas*. Historical records and the trace amounts captured in early demersal fish surveys (Alverson et al. 1964) contrast sharply with recent catches. Between 1963 and 1977, for example, total catches from 16 to 666 metric tons (t) were landed in Washington, Oregon, and northern California as compared with 19,526 t in 1980 (Demory[1]). Traditional demersal fish surveys have undersampled this species because of both its level of aggregation and its midwater habits (Alverson et al. 1964; Gunderson and Sample 1980) and have therefore not recognized the value of the resource. The increased importance of *S. entomelas* in the west coast trawl fishery has resulted in increased effort to obtain biological information necessary for management of the fishery (Lenarz and Gunderson[2]).

This note is intended to describe the fecundity of *S. entomelas* off Oregon as a function of length and weight, adding to the limited information available from samples collected in 1957 through 1959 and described by Phillips (1964).

Materials and Methods

Sebastes entomelas ovaries were collected in December 1980 and January 1981 during port sampling in Newport, Oreg., by the Oregon Department of Fish and Wildlife. All samples were taken from commercial midwater trawling vessels which had fished off central Oregon (lat. 42°30′ to 45°00′N). While the port sampling was random with respect to size, the samples selected for fecundity analysis were size stratified, and large and small samples were relatively overrepresented. Each specimen was measured to the nearest centimeter in fork length (FL) and weighed to the nearest 10 g; otoliths were removed for subsequent age determination. Ovaries used for fecundity estimates in the present study were those with yolked oocytes corresponding to maturity stage 3 of Barss and Echeverria,[3] although eggs were counted in a few fertilized ovaries which, when collected, showed no signs of extrusion. Whole ovaries were preserved in Gilson's solution modified as described in Gunderson et al. (1980). The solution was changed after approximately 1 wk, and after two more weeks the ovaries were teased apart with forceps and shaken at regular intervals to facilitate separation of ovarian tissue from oocytes. Finally, after approximately 3 mo, the ovaries were put through a coarse strainer under running water, which aided in separating oocytes from ovarian tissue.

Oocyte counts were made by the wet subsampling method (Bagenal and Braum 1968). Oocytes were placed in a beaker and the contents were diluted to a final volume dependent upon the size of the ovary, but varying from 200 to 2,000 ml. The oocytes and water were placed on a magnetic stirrer and stirred until a homogeneous mixture was obtained. Six subsamples (2 ml each) were taken by pipette and placed in vials. Three to six subsamples were counted (depending upon variability of the first three counts) under a binocular microscope. Since all ovaries were mature and within a month of fertilization, there was no difficulty in discerning and counting maturing oocytes. Fecundity was estimated by multiplying the mean number of maturing oocytes per milliliter by the volume of water and oocytes from which the subsamples were drawn.

Results and Discussion

Sixty-eight ovaries from *S. entomelas* were collected, three in December 1980 and 65 in January 1981. Four of the ovaries showed signs of fertilization; although counts were taken on these four specimens, they were not included in the fecundity estimates, which correspond to the "pre-fertilized" fecundity of Raitt and Hall (1967). The distribution of fish lengths for the fecundity samples is shown in Figure 1.

---

[1] Robert L. Demory, Oregon Department of Fish and Wildlife, Newport, OR 97365, pers. commun. January 1982.

[2] Lenarz, W. H., and D. R. Gunderson. 1980. Summary of the widow rockfish workshop. Unpubl. manuscr. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

[3] Barss, W. H., and T. Echeverria. 1980. Maturity of widow rockfish (*Sebastes entomelas*) from the northeastern Pacific, 1977-1981. Unpubl. manuscr. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

Mean diameter of the preserved, unfertilized oocytes was 0.814 mm and individual means ranged from 0.634 to 0.954 mm. The mean number of oocyte subsamples counted was 4.1 and ranged from 3 to 6. Coefficients of variation of the counts ranged from 0.6 to 10.2% with a mean of 4.6%. As expected, fecundity increased with increasing length, with estimates ranging from 95,375 oocytes at 33 cm FL to 1,113,000 oocytes at 52 cm FL (Fig. 2). Data were fit with linear regressions as used by Gunderson et al. (1980) and with power functions frequently used in fecundity-length relationships (Bagenal and Braum 1968; Raitt and Hall 1967). Although both equations were highly significant, the linear regression provided a slightly better fit to the data but may underestimate fecundity at lengths below about 36 cm FL. Only rarely, however, are females smaller than 35 cm FL sexually mature (Barss and Echeverria footnote 3). A linear relationship was also used to describe the weight-fecundity relationship (Fig. 3). The fitted equations are as follows:

Length

$$F = 59{,}182.4\ L - 1{,}999{,}200 \qquad r^2 = 0.90 \qquad N = 64$$

or

$$\log F = 5.431(\log L) - 3.19 \qquad r^2 = 0.89 \qquad N = 64$$

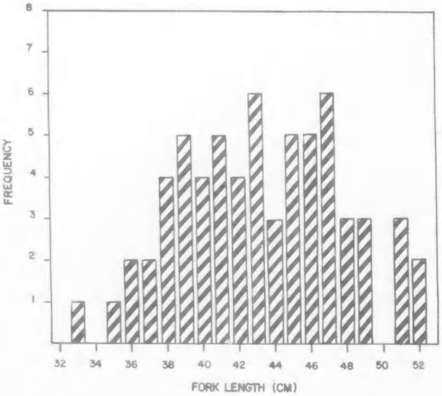


FIGURE 1.—Length-frequency of specimens of *Sebastes entomelas* used in estimating fecundity.

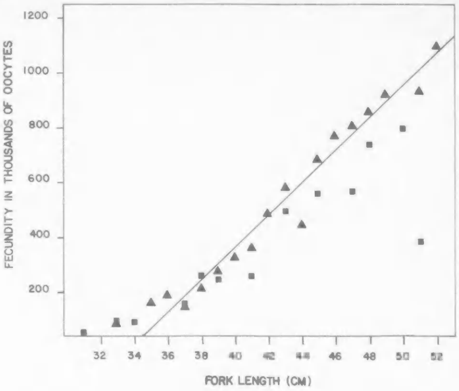


FIGURE 2.—Fecundity of *Sebastes entomelas* as a function of fork length (cm). Triangles represent mean values for fecundity from the present study and the line represents the fitted curve through these points. Squares represent mean values of fecundity from Phillips (1964) with lengths converted to the nearest cm FL. The relationship from the present study is significantly different from that of Phillips (analysis of covariance, $P<0.01$).

Weight

$$F = 605.71\ W - 261{,}830.7 \qquad r^2 = 0.91 \qquad N = 64$$

where F = fecundity (maturing oocytes), L = fork length (cm), W = weight (g), r^2 = coefficient of determination, and N = number of specimens. Fecundity of *S. entomelas* is thus relatively high within the genus *Sebastes*, with values similar to

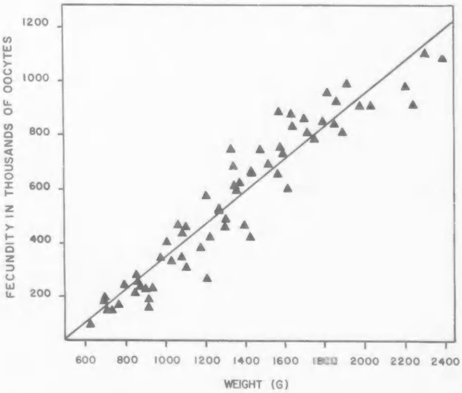


FIGURE 3.—Fecundity of *Sebastes entomelas* as a function of weight. Each point represents an individual specimen.

those of *S. flavidus* and *S. pinniger* at equivalent lengths (Gunderson et al. 1980). The mean value of weight-specific fecundity (389 eggs/g body weight) is also relatively high for this genus, as summarized by MacGregor (1970); this value should be considered carefully, however, since weight-specific fecundity is dependent upon size and age (Table 1).

TABLE 1.—Weight-specific fecundity (eggs/g body weight) by age class of *Sebastes entomelas* from the present study. N = number of specimens, SE = standard error of the mean. The mean age of specimens >15 yr is 21.5 yr.

Age (yr)	N	Specific fecundity (eggs/g)	SE
5	1	151.4	—
6	3	254.0	37.0
7	6	272.9	31.4
8	3	273.3	6.7
9	5	355.3	26.9
10	12	374.7	27.9
11	14	444.9	22.6
12	6	423.4	38.2
13	5	476.8	22.5
14	1	516.1	—
≥15	8	447.4	7.8

The length-fecundity and weight-fecundity relationships described in the present study differ significantly from data presented by Phillips (1964; analysis of covariance, $P<0.01$). The 20 fish in his study were collected from 1957 to 1959 in California. We converted the total length measurements in Phillips to fork length using the total length-fork length relationship in Lenarz[4] and plotted mean values by 1 cm length intervals for comparison with data from the present study (Fig. 2). Values are similar through approximately 40 cm FL, but at greater lengths the values from Phillips are more variable and generally lower than fecundity determined in the present study. Similarly, data on mean weight-specific fecundity was lower; MacGregor (1970) calculated a value of 288 eggs/g from Phillips' (1964) data. As stated above, the mean from the present study was 389 eggs/g. The weight-fecundity regression from Phillips (1964) is characterized by a lower slope. The lines intersect near 1,000 g and Phillips' estimate at 2,000 g is 67.5% of that predicted by the regression from the present study. Gunderson et al. (1980) noted a similar pattern of generally lower fecundity at greater lengths when comparing their data for *S. goodei* and *S. flavidus* with that of Phillips (1964). Since the methods in the present study are most similar to those of Gunderson et al. (1980), methodological differences could explain the different results. Geographic differences, however, may also be involved. Gunderson et al. (1980) noted increased fecundity at length for *S. goodei* in northern as compared with southern geographic regions. Clear differences are also apparent in the length at 50% maturity for several species of *Sebastes*, with maturity occurring earlier in southern areas. Barss and Echeverria (footnote 3), for example, noted that the length and age at 50% maturity for *S. entomelas* females are 38 cm FL and 7 yr off Oregon and 32 cm FL and 5 yr off California. Thus reproductive characteristics within species may differ between areas.

It is probable that *S. entomelas* spawns only once per year. While MacGregor (1970) noted evidence of multiple spawning in three species of *Sebastes*, these species were generally characterized by lower weight-specific fecundity than observed for *S. entomelas*. Furthermore, the lack of a secondary mode of oocytes and the distinct, relatively short spawning season noted by Barss and Echeverria (footnote 3) in both Oregon and California samples indicate a single spawning per year for this species.

Estimates of fecundity from the four samples of *S. entomelas* with fertilized ovaries were below values predicted from the weight-fecundity relationship; the percent of expected fecundity decreased with increasing developmental stage of embryo (Table 2). These specimens had no signs of extrusion of embryos during capture, but it cannot be ruled out. Raitt and Hall (1967), however, noted that egg counts from fertilized

TABLE 2.—Percentage of nonviable eggs and reduction in fecundity in the ovaries of four specimens of fertilized *Sebastes entomelas*. The percent nonviable eggs was determined in four subsamples of 300 eggs. Expected fecundity was determined from the weight-fecundity relationship.

Ovarian stage	% nonviable eggs (±2 SE)	Fecundity (% expected)
Newly fertilized	0.4 (0.17)	87
Late high blastula	1.0 (0.81)	62
Late high blastula	3.2 (0.79)	56
Eyed embryos	0.4 (0.17)	38

---

[4] Lenarz, W. H. 1980. Aging and growth of widow rockfish. Unpubl. manuscr. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

specimens of *S. marinus* were below those of nonfertilized specimens and suggested that the difference was related either to incomplete fertilization or to presence of nonviable eggs which are subsequently resorbed after fertilization. MacGregor (1970) observed undeveloped or unfertilized oocytes from the same batch as developing embryos in all species of *Sebastes* examined, but these accounted for only 0.06% of the egg count in *S. paucispinis*. In *S. entomelas*, this percentage was higher (Table 2). Moreover, since the percentage of expected fecundity decreases with later developmental stage, resorption of nonviable embryos may occur throughout the gestation period. Because estimated and realized fecundity may differ, Gunderson (1977) suggested that fecundity estimates of *S. alutus* be considered tentative. Foucher and Beamish (1980) have made similar suggestions concerning fecundity of the oviparous Pacific hake, noting that nonviable oocytes could contribute to overestimates of fecundity. In the genus *Sebastes* it would thus be interesting to determine fecundity in various stages of developing and fertilized ovaries in a shallow living species which could be captured with no fear of extrusion-related reductions in counts of fertilized eggs or embryos.

Acknowledgments

This work was supported by Contract Number 81-ABC-00144 from the National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Seattle, Wash. We thank the fishing industry in Newport, Oreg., for cooperation with sampling and catch information and R. L. Demory and W. H. Lenarz for their helpful comments on the manuscript. We also thank W. H. Lenarz for supplying ages for the specimens from this study and Karen Dykes for typing the drafts of the manuscript.

Literature Cited

Alverson, D. L., A. T. Pruter, and L. L. Ronholt.
1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lecture Series on Fisheries. Inst. Fish. Univ. B.C., Vancouver, 190 p.

Bagenal, T. B., and E. Braum.
1968. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 159-181. Int. Biol. Programme Handb. 3.

Foucher, R. P., and R. J. Beamish.
1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37: 41-48.

Gunderson, D. R.
1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region, and their response to fishing. Fish. Bull., U.S. 75:369-403.

Gunderson, D. R., P. Callahan, and B. Goiney.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4):74-79.

Gunderson, D. R., and T. M. Sample.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42(3-4):2-16.

MacGregor, J. S.
1970. Fecundity, multiple spawning, and description of the gonads in *Sebastodes*. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 596, 12 p.

Phillips, J. B.
1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

Raitt, D. F. S., and W. B. Hall.
1967. On the fecundity of the redfish, *Sebastes marinus* (L.). J. Cons. 31:237-245.

George W. Boehlert

Oregon State University
Marine Science Center
Newport, OR 97365

W. H. Barss

Oregon Department of Fish and Wildlife
Newport, OR 97365

P. B. Lamberson

Oregon State University
Marine Science Center
Newport, OR 97365

A COMPARATIVE STUDY OF AUTOCHTHONOUS BACTERIAL FLORA ON THE GILLS OF THE BLUE CRAB, *CALLINECTES SAPIDUS*, AND ITS ENVIRONMENT[1]

The bacterial flora of blue crabs, *Callinectes sapidus*, has been previously enumerated and identified by examining blue crab hemolymph (Tubiash et al. 1975; Sizemore et al. 1975; Colwell et al. 1975). Other studies on live blue crabs

---

[1] Contribution No. 82-17C of the Southeast Fisheries Center Charleston Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 12607, Charleston, SC 29412-0607.

FISHERY BULLETIN: VOL. 80, NO. 4, 1982.

have been concerned with the presence of specific human or fishery pathogens in the hemolymph, necrotic tissue, or gill material (Rosen 1967; Williams-Walls 1968; Krantz et al. 1969; Cook and Lofton 1973; Johnson 1976). The statement of Tubiash et al. (1975) that the hemolymph of most healthy blue crabs contains a natural or autochthonous bacterial flora has been challenged, and it has been suggested that further experiments using minimally stressed crabs would be needed to substantiate that statement (Johnson 1976).

This study was designed to determine, seasonally, the natural *Vibrio*, fecal coliform, and aerobic, heterotrophic bacterial populations on blue crabs from environments that differed in salinity and influx of urban and industrial pollutants. These microbial populations were also compared with those found in intertidal oysters (*Crassostrea virginica*), waters, and sediments collected simultaneously with the crabs. Blue crab gills were chosen as a suitable substrate for microbiological investigations because they have direct contact with the environment and are easily sampled and processed for enumeration of their bacterial flora.

Materials and Methods

Two South Carolina areas, Charleston harbor and St. Helena Sound, an estuary 35 mi south of Charleston, were surveyed during a 22-mo period between August 1979 and May 1981 (Fig. 1). Within each area, two sampling stations were selected, representing mean salinities of 10‰ and 25‰. The Charleston harbor sampling stations were Foster Creek, salinity 10‰, a tributary to the Wando River, which, along with the Ashley and Cooper Rivers, forms Charleston harbor; and Shutes Folly Island, salinity 25‰, situated near the center of Charleston harbor. The oyster beds in both sites are closed to harvesting because fecal coliform levels, monitored in the water column and oyster meats by the South Carolina Department of Health and Environmental Control, exceed safe limits for harvesting areas. Foster Creek receives negligible industrial pollution, whereas the Shutes Folly Island station receives a moderate-to-heavy influx of industrial pollutants. The St. Helena Sound stations were the Ashepoo River at Mosquito Creek, salinity 10‰, and St. Helena Sound at the mouth of Rock Creek, salinity 25‰. Shellfish beds at these stations are open to harvesting, with no discernible influx of urban, industrial, or commercial pollutants. Each station was sampled on a quarterly basis to coincide with the highest and lowest temperatures in the water column and during the middle of the two transitional periods in water temperatures.

Blue crabs were captured in commercial-type crab pots baited with fresh fish heads. The crab pots were harvested from 4 to 24 h after being set, dependent on the seasonal rate of blue crab capture. Intertidal oysters and sediments from the oyster beds were collected manually at low tide. Two hundred grams of the top centimeter of sediment were removed with sterile tongue depressors and placed in sterile containers. Surface water samples (1 m below the surface) were collected with a Niskin[2] sterile bag sampler (General Oceanics, Miami, Fla.) at the site of blue crab collections. All sediment, water, and oyster samples were immediately cooled with ice. Blue crabs were maintained at their in situ temperature by placing them in a thermally insulated container. All samples were analyzed within 4 to 8 h. During a survey, two to four representative composite samples of blue crab gills (dependent on seasonal activity of blue crabs), three oyster composites, and two samples each of sediment and surface water were collected and analyzed for each sampling station. A composite gill sample contained gills from 10 to 12 crabs. Since mature female blue crabs migrate to higher salinities, male blue crabs dominated the population at 10‰ salinity and females at 25‰ salinity. Whenever possible, blue crabs above the legal harvesting size for South Carolina, 127 mm, were sampled. Each survey was completed within 4 d. For monitoring purposes, temperature and salinity of the surface water were measured, using a YSI Model 33 Salinity-Conductivity-Temperature meter (Yellow Springs Instrument Co., Yellow Springs, Ohio).

Preparation of oyster and water samples for analyses followed standard procedures (American Public Health Association 1970, 1976). Carapaces of the blue crabs were cracked vertically with a blow from a stainless steel knife. The knife did not penetrate into the gut or organs. The carapace was then removed by pulling up on the lateral spines (Fig. 2). Exposed gills were aseptically removed with forceps and placed in

---

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

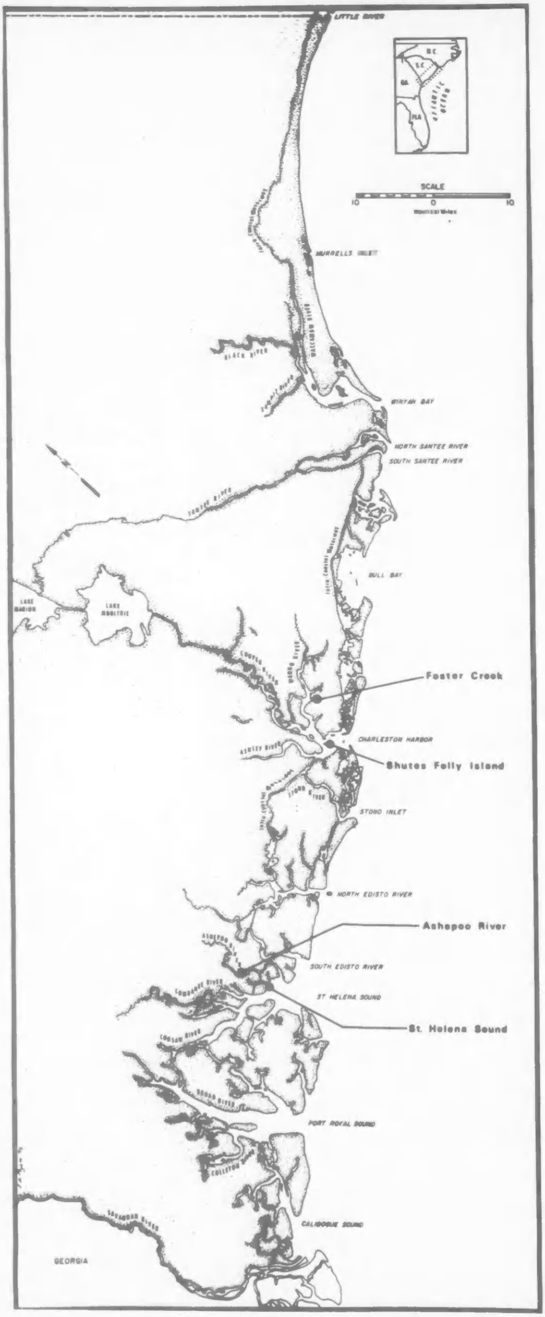

LITTLE RIVER
N.C.
S.C.
GA.
FLA.
ATLANTIC OCEAN
SCALE
10
0
10
Nautical Miles
MURRELLS INLET
BLACK RIVER
SAMPIT RIVER
WINYAH BAY
NORTH SANTEE RIVER
SOUTH SANTEE RIVER
SANTEE RIVER
BULL BAY
LAKE MARION
LAKE MOULTRIE
COOPER RIVER
WANDO RIVER
Foster Creek
CHARLESTON HARBOR
ASHLEY RIVER
Shutes Folly Island
STONO RIVER
STONO INLET
NORTH EDISTO RIVER
Ashepoo River
SOUTH EDISTO RIVER
COMBAHEE RIVER
ST HELENA SOUND
St. Helena Sound
COOSAW RIVER
BROAD RIVER
PORT ROYAL SOUND
COLLETON RIVER
CALIBOGUE SOUND
SAVANNAH RIVER
GEORGIA

FIGURE 1.—Map of coastal South Carolina showing location of sampling stations.

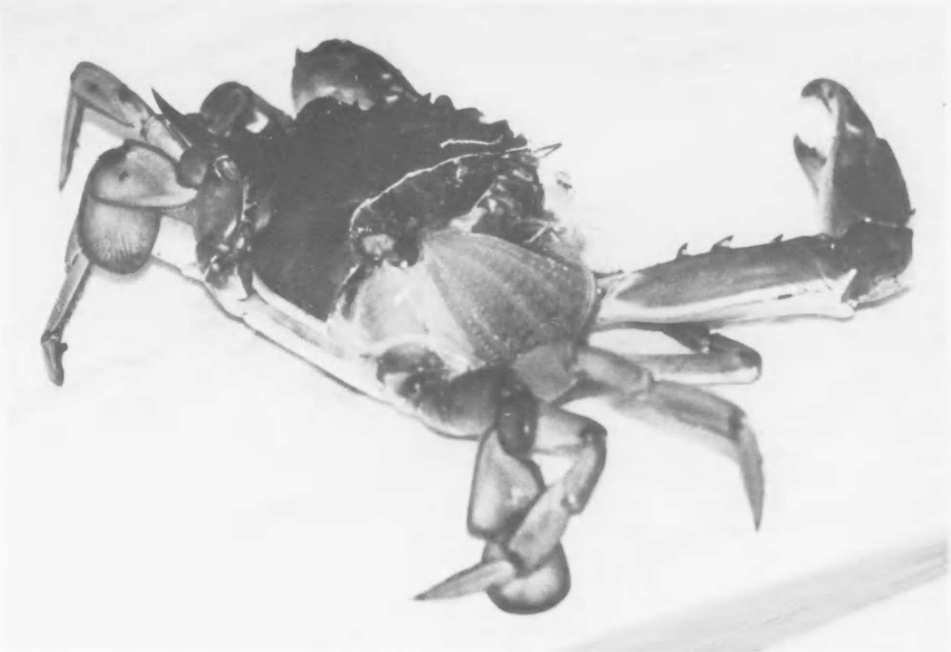


FIGURE 2.—Photograph of blue crab with section removed from vertically cracked carapace.

sterile containers. The blue crab gills were homogenized in a blender for 2 min at high speed and further prepared for bacterial analysis following the standard procedure for oysters. Blue crab gills and oysters were analyzed on a wet-weight basis (50 g), but sediments were analyzed on a volume-to-volume basis (50 ml) because of the great differences in sediment densities found in the environment. The initial dilution was made by volume displacement of the diluent by the sediment in a calibrated container as previously described (Babinchak et al. 1977). All dilutions were made using sterile 0.1% peptone (Difco Laboratories, Detroit, Mich.) saline solution (1.5% NaCl).

Total viable, aerobic, heterotrophic bacterial counts for all samples were determined, using the spread-plate technique and a modification of a low-nutrient, artificial seawater plating medium (ASWLN) of Litchfield et al. (1975) containing the following ingredients per liter of half-strength artificial seawater (Rila Marine Mix, Teaneck, N.J.): 0.5 g peptone (Difco), 0.5 g yeast extract (BBL Microbiology Systems, Cockeysville, Md.), 0.1 g sodium glycerophosphate (MCB Manufacturing Chemist, Inc., Cincinnati, Ohio), and 20 g agar (BBL). Three replicates of each dilution were plated, and the inoculated plates incubated at 20°C for 14 d.

Fecal coliform counts in all samples were estimated by the three-tube most-probable-number (MPN) procedure prescribed for seawater and tissues (American Public Health Association 1970, 1976). Lauryl sulfate tryptose broth (BBL) was used in the presumptive test, with confirmation in EC broth (BBL) incubated at 44.5°C in a circulating water bath.

Vibrio-like organisms were enumerated on thiosulfate citrate bile salts agar (TCBS; BBL) using the spread-plate technique for all samples. Fifteen to thirty colonies, representing all colonial types, as determined with oblique or darkfield illumination through a stereomicroscope, were picked only from the blue crab gill-inoculated TCBS plates. The cultures were purified and then characterized biochemically using the API 20E system (Analytab Products, Inc., Plainview, N.Y.).

Results

During the initial survey, it was noted that many intermolt blue crabs had dark brown or mahogany-colored gills which contrasted with the light-colored gills of recently molted crabs. The light- and dark-colored gill material was subsequently divided and analyzed separately.

The microbiological data from 61 blue crab gill samples collected during five quarterly surveys were analyzed statistically using a generalized analysis of variance (ANOVA) employing the maximum likelihood approach. The dependent variables for analysis were the microbial counts on the blue crab gills; independent variables were urban and industrial pollution, salinity, season, gill color, and their pairwise interactions. In Table 1, the *P*-values resulting from the analysis of variance indicated that season, gill color, and the interaction of pollution and season affected the total *Vibrio* and aerobic, heterotrophic bacterial counts. Fecal coliform counts were not significantly affected by any of the variables investigated.

Graphically displayed in Figure 3 is the effect of season and gill color on total *Vibrio* and aerobic, heterotrophic bacterial counts. Dark gills had consistently higher counts, and the counts showed a similar pattern with season.

Surprisingly, the absence of urban fecal pollution had no significant impact on fecal coliform counts in blue crab gills (Table 1). Blue crab gills obtained from St. Helena Sound, a pristine area, yielded high fecal coliform counts, whereas intertidal oysters and waters sampled concurrently were relatively free of contamination (Table 2). To confirm the identity of the fecal coliforms found in St. Helena Sound, 90 bacteria were isolated from positive EC broth MPN tubes, checked for their Gram reaction, and analyzed biochemically with the four reactions which constitute the IMViC differential test (American Public Health Association 1976). The sources for the bacterial isolates were blue crab gills (35), water (26), sediment (15), and oysters (14). Ninety-four percent of the isolates were identified as typical *Escherichia coli* and 6% as typical *Enterobacter aerogenes*. Twenty fecal coliforms isolated from blue crab gills were also tested with the API 20E system, and all identified as *E. coli*. Representative samples of blue crab stomach contents analyzed in parallel with the

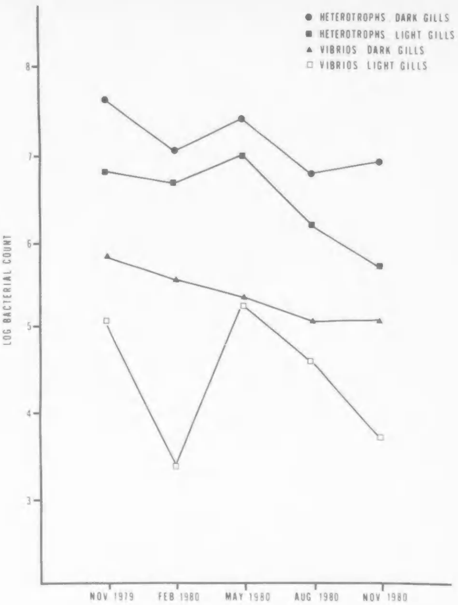


FIGURE 3.—Average total *Vibrio* and heterotrophic bacterial counts per gram of light and dark crab gill tissue from all samples collected from the St. Helena Sound area.

TABLE 1.—*P* values resulting from generalized ANOVA of crab gill data. The hypothesis that a factor has an effect on microbial counts in blue crab gills is accepted when $P \leq 0.05$.

Independent variables	*P*-values, dependent variables		
	Heterotrophs	*Vibrio*	Fecal coliforms
Pollution	0.748	0.233	0.304
Salinity	0.549	0.207	0.211
Season	0.030	0.015	0.355
Gill color	0.001	0.001	0.312
Pollution - salinity	0.916	1	1
Pollution - season	0.001	0.036	1
Pollution - gill color	1	1	1
Salinity - season	1	1	1
Salinity - gill color	1	1	1
Season - gill color	1	1	1

TABLE 2.—Distribution of fecal coliforms in samples collected from St. Helena Sound area.

Sample	Fecal coliforms/100 g[1]				
	Nov. 1979	Feb. 1980	May 1980	Aug. 1980	Nov. 1980
Intertidal oysters	21	12	12	21	160
Water	80	5	2	16	12
Sediment	430	340	60	19	90
Blue crab gills	2,000	4,300	230	4,300	210

[1] 100 ml of water and sediment samples.

corresponding gill tissues gave significantly lower heterotrophic counts.

Dark blue crab gills harbored the same heterotrophic bacterial populations found in the sediments (Fig. 4). Similar results with total *Vibrio* populations were obtained in these areas. As shown in Figure 4, oysters and water contained lower heterotrophic counts.

Only 10 to 30% of the TCBS bacterial isolates from individual samples of light and dark gills could be identified to genus and species using the API identification system. *Aeromonas* spp. made up 28% of those TCBS isolates identifed.

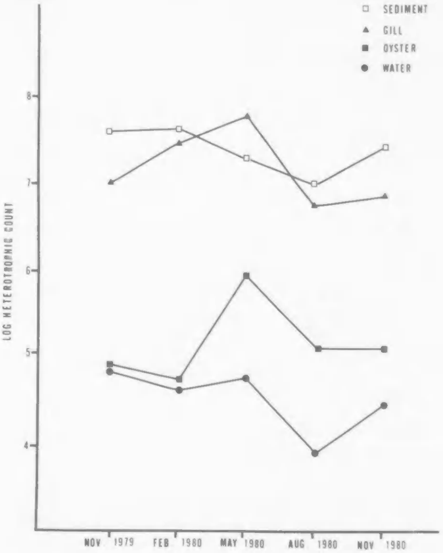


FIGURE 4.—Average heterotrophic bacterial counts per gram of sample collected quarterly from Foster Creek.

Discussion

Common external features which distinguish blue crabs with brown to mahogany gills are rust-spotted exoskeletons and, occasionally, attached barnacles and algae. These conditions are not considered abnormal for late intermolt crabs. Johnson (1977) has also described a viral disease in which blue crabs displayed similar diagnostic signs: failure to molt, a brown-spotted exoskeleton, and gills that were often red-brown.

Sections made from dark gills collected during the survey showed that these gills were, to varying degrees, fouled by a layer of bacteria and mucus (P. T. Johnson[3]). Observations of similarly fouled gills of rock crabs, using scanning electron microscopy, showed large numbers of bacteria residing on the gill tissue, similar to those found on blue crab gills in this study using bacterial enumeration procedures (F. Thurberg[4]).

These enumeration data suggest that the gills of blue crabs provide an ecological niche for the growth and physiological activity of heterotrophs, *Vibrio* spp., and related organisms, equivalent to that described for sediments and zooplankton (Kaneko and Colwell 1975 a, b, 1978). The high fecal coliform population found in our pristine area would indicate that gill surfaces also provide a protective ecological niche much like that reported for marine sediments, where high fecal coliform populations can accumulate and persist even in ecosystems where influx of fecal coliforms is low (Rittenburg et al. 1958; Van Donsel and Geldreich 1971; Babinchak et al. 1977).

Urban and industrial pollution did not have an effect on total *Vibrio* and aerobic, heterotrophic bacterial counts on blue crab gills. Since these two microbial populations are indigenous and dependent on nutrient levels for growth, industrial and domestic pollution would not necessarily have shown an effect over the pristine areas sampled. The vast marshlands which drain into the St. Helena Sound area (Tiner 1977) would introduce large natural levels of dissolved and particulate organic material and other nutrients which could support the high bacterial levels observed.

The low rates of identification by the API 20E system can be attributed primarily to the high percentage of clinical bacterial isolates which form the API data base. Even some of our positive identifications are now in question, because marine isolates identified as *Aeromonas* spp. with the API system are known to be Group F vibrios (Seidler et al. 1980). This group of *Vibrio*-like organisms has been associated with diarrheal illness, although the epidemiology of the disease has not been well-defined.

---

[3] P. T. Johnson, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Oxford, MD 21654, pers. commun. 1981.

[4] F. Thurberg, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Milford, CT 06460, pers. commun. 1981.

The data obtained in this study establish blue crab gills as excellent surfaces for enumerating the blue crab's natural adherent bacterial population. Bacterial quantitation, which is difficult to achieve with other crab surfaces, is easily accomplished with gills. Succession of bacterial species and the possible influence of environmental contaminants in the bacterial colonization of blue crab gills are also conveniently accommodated by the molting process. The freshly molted gill surfaces can be compared with gills that have been exposed to the environment for extended periods. Gill surfaces may provide a model system for monitoring biological or chemical pollutants based on observable changes in the autochthonous bacterial populations of blue crab gills.

Acknowledgments

The authors thank L. Ng for statistical analysis of the data and V. Ward and D. Green for their technical assistance.

Literature Cited

AMERICAN PUBLIC HEALTH ASSOCIATION.

1970. Recommended procedures for the examination of sea water and shellfish. 4th ed. Am. Public Health Assoc., Inc., Wash., D.C.

1976. Compendium of methods for the microbiological examination of foods. Am. Public Health Assoc., Inc., Wash., D.C.

BABINCHAK, J. A., J. T. GRAIKOSKI, S. DUDLEY, AND M. F. NITKOWSKI.

1977. Distribution of faecal coliforms in bottom sediments from the New York Bight. Mar. Pollut. Bull. 8: 150-153.

COLWELL, R. R., T. C. WICKS, AND H. S. TUBIASH.

1975. A comparative study of the bacterial flora of the hemolymph of *Callinectes sapidus*. Mar. Fish. Rev. 37 (5-6):29-33.

COOK, D. W., AND S. R. LOFTON.

1973. Chitinoclastic bacteria associated with shell disease in *Penaeus* shrimp and the blue crab (*Callinectes sapidus*). J. Wildl. Dis. 9:154-159.

JOHNSON, P. T.

1976. Bacterial infection in the blue crab, *Callinectes sapidus*: Course of infection and histopathology. J. Invertebr. Pathol. 28:25-36.

1977. A viral disease of the blue crab, *Callinectes sapidus*: Histopathology and differential diagnosis. J. Invertebr. Pathol. 29:201-209.

KANEKO, T., AND R. R. COLWELL.

1975a. Adsorption of *Vibrio parahaemolyticus* onto chitin and copepods. Appl. Microbiol. 29:269-274.

1975b. Incidence of *Vibrio parahaemolyticus* in Chesapeake Bay. Appl. Microbiol. 30:251-257.

1978. The annual cycle of *Vibrio parahaemolyticus* in Chesapeake Bay. Microb. Ecol. 4:135-155.

KRANTZ, G. E., R. R. COLWELL, AND E. LOVELACE.

1969. *Vibrio parahaemolyticus* from the blue crab *Callinectes sapidus* in Chesapeake Bay. Science (Wash., D.C.) 164:1286-1287.

LITCHFIELD, C. D., J. B. RAKE, J. ZINDULIS, R. T. WATANABE, AND D. J. STEIN.

1975. Optimization of procedures for the recovery of heterotrophic bacteria from marine sediments. Microb. Ecol. 1:219-233.

RITTENBERG, S. C., T. MITTWER, AND D. IVLER.

1958. Coliform bacteria in sediments around three marine sewage outfalls. Limnol. Oceanogr. 3(1):101-108.

ROSEN, B.

1967. Shell disease of the blue crab, *Callinectes sapidus*. J. Invertebr. Pathol. 9:348-353.

SEIDLER, R. J., D. A. ALLEN, R. R. COLWELL, S. W. JOSEPH, AND O. P. DAILY.

1980. Biochemical characteristics and virulence of environmental group F bacteria isolated in the United States. Appl. Environ. Microbiol. 40:715-720.

SIZEMORE, R. K., R. R. COLWELL, H. S. TUBIASH, AND T. E. LOVELACE.

1975. Bacterial flora of the hemolymph of the blue crab, *Callinectes sapidus*: Numerical taxonomy. Appl. Microbiol. 29:393-399.

TINER, R. W., JR.

1977. An inventory of South Carolina's coastal marshes. S.C. Mar. Resour. Cent. Tech. Rep. 23, 33 p.

TUBIASH, H. S., R. K. SIZEMORE, AND R. R. COLWELL.

1975. Bacterial flora of the hemolymph of the blue crab, *Callinectes sapidus*: Most probable numbers. Appl. Microbiol. 29:388-392.

VAN DONSEL, D. J., AND E. E. GELDREICH.

1971. Relationships of salmonellae to fecal coliforms in bottom sediments. Water Res. 5:1079-1087.

WILLIAMS-WALLS, N. J.

1968. *Clostridium botulinum* type F: Isolation from crabs. Science (Wash., D.C.) 162:375-376.

JOHN A. BABINCHAK
DANIEL GOLDMINTZ
GARY P. RICHARDS

Southeast Fisheries Center Charleston Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 12607, Charleston, SC 29412-0607

WHITE SHARK PREDATION ON PINNIPEDS IN CALIFORNIA COASTAL WATERS

White sharks, *Carcharodon carcharias*, prey on various fishes, sea turtles, whales, dolphins, and on several species of pinnipeds (Allen 1880; Elliot 1881; McCormick and Allen 1963; Davies 1964; Nishiwaki 1972; Ellis 1976; Ainley et al. 1981; McCosker 1981). Data on pinnipeds preyed upon by sharks in California waters are meager and many aspects of the predator-prey relationship are unknown.

Four types of evidence indicate that sharks prey on pinnipeds: 1) Pinniped remains in the stomachs of dead sharks, 2) observation of seals with injuries inflicted by large sharks, 3) observation of shark attacks on seals, and 4) the presence of sharks near seal rookeries at a time when seals are present. We report evidence of the first two kinds regarding shark predation on northern elephant seals, *Mirounga angustirostris*, and harbor seals, *Phoca vitulina*.

Methods

Five white sharks caught in southern California waters in 1975 and 1976 and two white sharks that washed ashore in central California in 1977 and 1978 were examined. The fresh dead sharks were weighed, measured, and their sex determined. Stomachs were dissected out and contents identified, and in some cases, weighed and measured (Table 1).

From 1968 to 1980, shark-bitten elephant seals on Año Nuevo Island and the adjacent Año Nuevo Mainland in central California were counted, photographed, and identified individually, and their behavior was monitored. This was accomplished during daily censuses conducted each breeding season from December to mid-March and during weekly censuses conducted during the remainder of the year. Only seals with fresh wounds judged by their pink or bloody appearance to be less than a few days old were included in the sample. This gives us confidence that our subjects were injured near the study area. We did not census animals with old scars or healed injuries, whose origins were difficult to ascertain. Shark injuries were differentiated from other wounds, caused by boat propellers or intraspecific fighting, by their oval shape and the jagged serrations caused by the predator's sharp teeth. Both slight and serious wounds were included. Slight wounds consisted of superficial tooth punctures or scrapes across the skin; serious wounds involved deep bites and tears. Seriously wounded seals had large flaps of flesh exposed or chunks of flesh missing. The dimension of bites was measured on a few dead seals.

We marked and followed 11 females who sustained moderate to severe shark wounds when pregnant just before arriving on the island to give birth. Their pups were marked at birth and the pair was observed until the filial relationship ended. Northern elephant seal females give birth within a week after arriving on the rookery. A female nurses her pup daily for about 4 wk before weaning it and returning to sea (Le Boeuf et al. 1972).

A similar search for shark-bitten harbor seals, which breed at Año Nuevo Island and numerous

TABLE 1.—Stomach contents of white sharks collected off the California coast from 1975 to 1978. Specimens 1-5 were collected by Sea World of San Diego, no. 6 by K. Skaug and M. Riedman, and no. 7 by an anonymous fisherman.

Specimen number	Date of collection	Location	Sex	Total length (m)	Weight of shark (kg)	Stomach contents
1	24 June 1975	8 km northeast of Santa Catalina Island	F	3.9	623.7	Anterior portion of stomach contained harbor seal remains (18.2 kg). Posterior stomach held unidentified pinniped.
2	1 Aug. 1975	110 m west of Laguna Beach	F	2.4	138.8	A 4-in patch of pinniped pelage.
3	6 Sept. 1975	Near Anacapa Island	F	4.9	1,428.8	Harbor seal, well digested.
4	7 Sept. 1975	11.3 km southeast of Anacapa Island	F	5.0	1,560.4	Skull and posterior portion of a juvenile elephant seal, plus large amounts of fur and digested material.
5	13 June 1976	West end of Catalina Island	F	5.5	1,882.4	Nearly digested. Bulk suggested a large animal, probably a marine mammal.
6	3 Feb. 1977	Año Nuevo Bay	F	4.7	?	Approximately one-third of a recently eaten 4-yr-old male elephant seal.
7	25 Sept. 1978	1.6 km offshore near Aptos	M	3.9	540	The head of a harbor seal.

other locations along the California coast, was not conducted.

Results

Table 1 summarizes data obtained from the stomachs of seven great white sharks examined shortly after they washed ashore dead or were captured at sea. Four points are worth noting:

1) Six stomachs contained seal remains, three of harbor seals and two of northern elephant seals.
2) Large prey was consumed. On the basis of tooth annuli and head and proboscis size, we estimate that specimen no. 6 (Fig. 1) contained the remains of a male elephant seal, 4 to 5 yr old. Intact, this seal would have measured approximately 3 m in length and weighed 450 to 680 kg.
3) The dimensions of the barely digested material in four of the shark stomachs indicate that the prey had been consumed in large pieces. For example, the stomach of one specimen contained the entire head, unmarred and severed cleanly at the neck. Both hindflippers and the tail were covered with hair and still attached to a segment of the sacrum. Also included were both foreflippers, one attached to a large piece of flesh containing the shoulder, a large portion of the midsection including six vertebrae, and several pieces of flesh and fur in various stages of decomposition. The elephant seal material weighed about 225 kg.
4) Six of the seven sharks were females.

The majority of the shark-injured elephant seals were observed during the winter breeding season. Only two recently bitten animals were observed on Año Nuevo Island in spring, despite the larger number of animals present at this time compared with the breeding season (Le Boeuf and Bonnell 1980).

Fewer than three victims per breeding season were observed from 1968 to 1976. From 1976 to

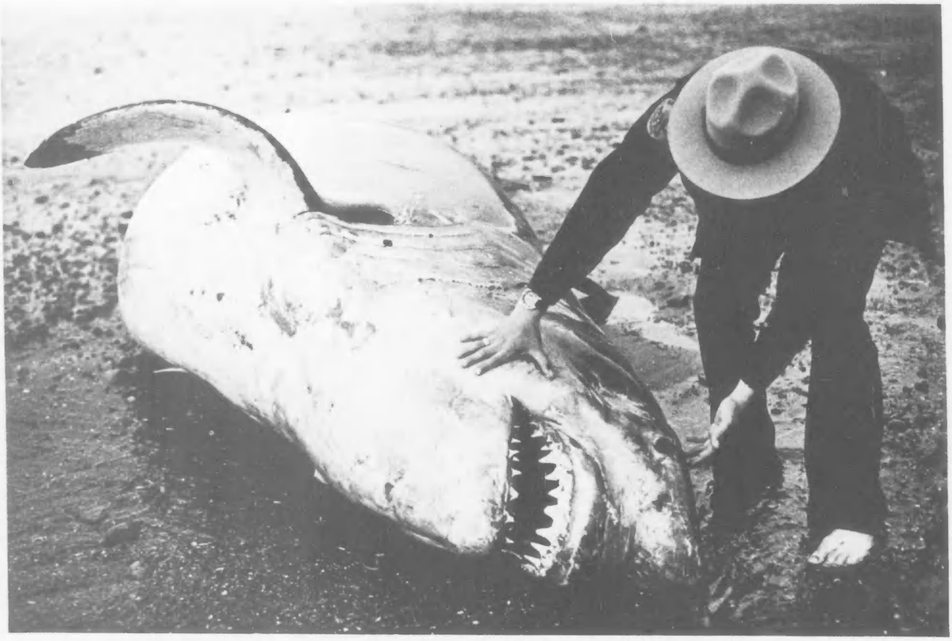


FIGURE 1.—A moribund great white shark (Specimen No. 6 in Table 1) that washed ashore near Año Nuevo Point shortly after having consumed approximately one-third of a young male northern elephant seal.

1980, 44 elephant seals with shark-inflicted injuries were observed (Table 2). Most of the elephant seals bearing recent shark wounds were adults. Males incurred the highest injury rate. Even the largest adult bulls, measuring more than 4.9 m and weighing between 1,800 and 2,700 kg were observed with shark bites (see Figure 2a). This may be due to the male habit of spending more time in the water near the rookery during the breeding season than females.

TABLE 2.—Shark-bitten northern elephant seals observed on Año Nuevo Island and the Año Nuevo Mainland.

Year	Adult males	Adult females	Juveniles	Pups	Total
1976		3			3
1977	3	4		1	8
1978	1	7	1		9
1979	5	1	1		7
1980	16	1			17
Total	25	16	2	1	44

Shark bites were located on diverse areas of the body but rarely on the head (Fig. 2). Possibly, frontal attacks were less successful or head bitten seals simply did not survive the encounter. In many cases, large pieces of blubber were missing or hung loosely from the animal. Some seals lost a foreflipper or hindflipper and in one case most of the proboscis. Some animals were bitten several times.

The majority of injured seals survived and recuperated rapidly. Infected wounds were rarely observed. Only three elephant seals died on the island or on the mainland following shark injury. In September 1976, an 8½-mo-old female was found dead with numerous deep lacerations and teeth marks covering her body. In December 1977, a 1-wk-old pup washed up with its entire sacral region amputated just below the umbilicus. In February 1978, a large 7-yr-old male died on the island's main breeding beach from massive shark wounds incurred within the previous 24 h. The most serious wounds consisted of two large oval chunks of flesh missing from the left side of the thoracic region (Fig. 2e). The bites measured 61 and 69 cm wide, 61 cm high, and 30 cm deep. No bite penetrated the body cavity although some muscle was removed and a rib was partly exposed.

Most female elephant seals bitten by sharks shortly before giving birth failed to wean their pups successfully. One female gave birth to a stillborn and returned to sea immediately. Seven females either abandoned their pups shortly after parturition or they were unable to care for them adequately. Four of these pups died; the eventual status of the other three pups could not be determined. The three females who were successful in weaning their pups appeared to have sustained the least serious injuries. All injured females remained in the harem for a much shorter period than normal. No injured female was observed to copulate, as uninjured females do, just before returning to sea. Thus, most injured females not only failed to produce a pup during the year of injury, but if they failed to copulate, they did not reproduce in the subsequent year as well.

Discussion

The data on stomach contents of white sharks presented in this paper is conclusive evidence that this shark preys on elephant seals and harbor seals in southern and central California waters.

We hypothesize that shark-inflicted injuries to northern elephant seals at Año Nuevo were caused primarily by white sharks. This hypothesis is supported by:

1) Data from a white shark that washed ashore at Año Nuevo Bay whose stomach contained the remains of an elephant seal (Table 2).
2) Observation of white sharks in the area. Twice during the summer of 1970 seal researchers saw white sharks measuring about 4.5 m from a dinghy 100 m south of the island. Party boat operators and fishermen reported seeing white sharks in this area several times during the last decade. Anglers report that white sharks occasionally attack large lingcod, *Ophidon elongatus*, when they are caught on hook and line; the sharks surface and circle boats, especially when fishing stops (Miller and Collier 1980).
3) An observed white shark attack of a northern elephant seal near Año Nuevo Island. This occurred on 1 February 1981.
4) The large size of shark bites. This indicates that they were caused by large sharks. White sharks may also be responsible for injuries to elephant seals on other rookeries in California (Ainley et al. 1981) and in Mexico (Townsend 1885; B. Le Boeuf, pers. obs.).

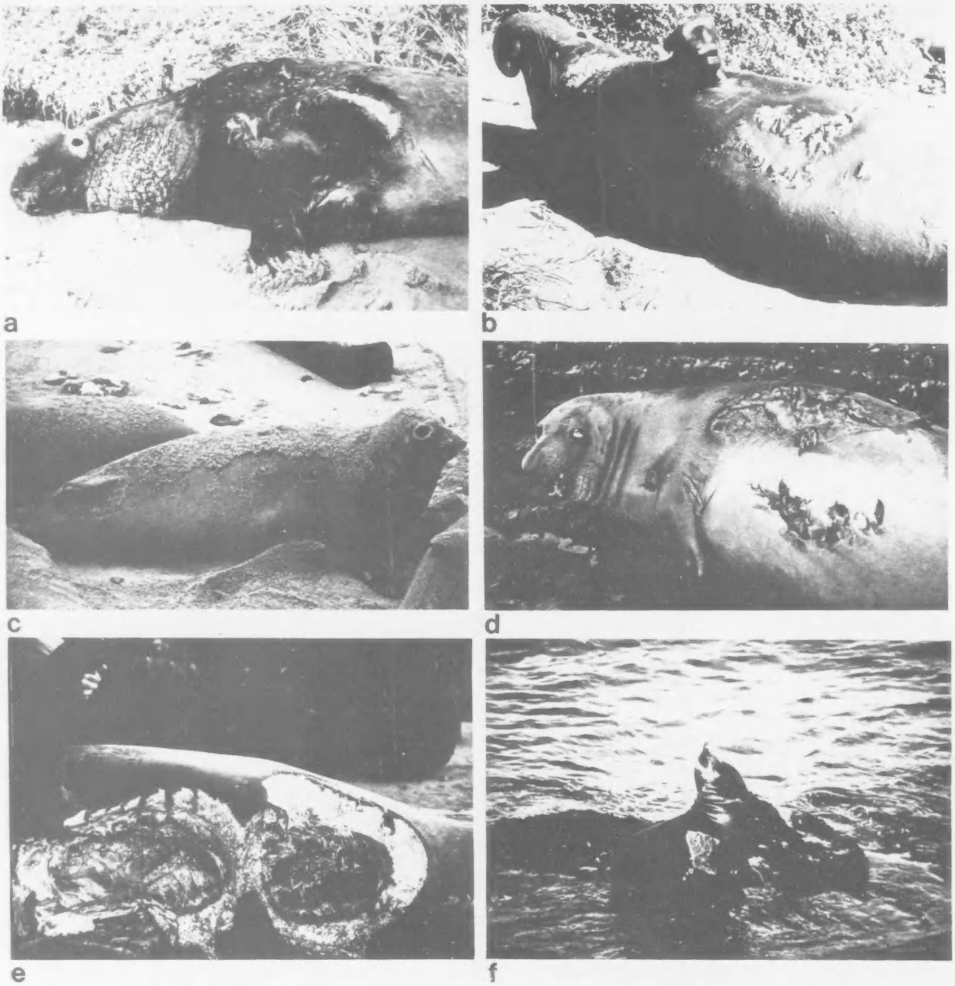


FIGURE 2.—A variety of shark-inflicted wounds observed on elephant seals and sea lions at Año Nuevo. A crescent shaped wound (a) and toothprints (b) on adult male elephant seals. A crescent bite on the dorsal posterior of an adult female elephant seal (c) and a large imprint of both jaws on an adult female with a blind left eye (d). Two large chunks of flesh bitten off the left side of an adult male elephant seal who subsequently died from his wounds (e). A California sea lion bearing a recently inflicted shark injury (f).

The results of this study support and augment those of Ainley et al. (1981) on South Farallon Island near San Francisco, Calif. They found that white sharks were responsible for most of the shark attacks observed on pinnipeds in the waters surrounding the island during the period September 1970 to February 1979. Northern elephant seals were attacked more frequently than harbor seals and sea lions, and shark-bitten female elephant seals exhibited low reproductive success.

Shark attacks on elephant seals of Año Nuevo Island and South Farallon Island (Ainley et al. 1981) appear to be increasing, but more data based on continued monitoring is necessary to confirm this point. Periodic increases in shark attacks of the magnitude found in these two studies may be related to several possible factors: The well-documented increase in elephant seals (Le Boeuf and Bonnell 1980), an increase in abundance of sharks, or to one or a few relatively inept predators at work.

Acknowledgments

We thank Sea World of San Diego for permitting us to use data from their shark collecting expeditions; Walter Ward for bringing the beached shark to our attention and for providing measurements; Keith Skaug, C. Leo Ortiz, Robert Gisiner, and Anne Hoover in acquiring and examining shark stomach contents; and Jack Ames, Ellen Chu, Daniel Miller, and Breck Tyler for comments on the manuscript. This study was supported in part by the National Science Foundation grant BNS 74-01363 402 to B. J. Le Boeuf.

Literature Cited

AINLEY, D. G., C. S. STRONG, H. P. HUBER, T. J. LEWIS, AND S. H. MORRELL.
1981. Predation by sharks on pinnipeds at the Farallon Islands. Fish. Bull., U.S. 78:941-945.

ALLEN, J. A.
1980. History of North American pinnipeds: A monograph of the walruses, sea-lions, sea-bears and seals of North America. Gov. Print. Off., Wash., D.C., 785 p.

DAVIES, D. H.
1964. About sharks and shark attack. Brown, Davis, and Platt Ltd., Durban, 237 p.

ELLIOTT, H. W.
1881. The seal-islands of Alaska. Gov. Print. Off., Wash., D.C., 176 p.

ELLIS, R.
1976. The book of sharks. Grossett and Dunlap, N.Y., 320 p.

LE BOEUF, B. J., AND M. BONNELL.
1980. Pinnipeds of the California islands: abundance and distribution. *In* D. Power (editor), The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, Calif.

LE BOEUF, B. J., R. J. WHITING, AND R. F. GANTT.
1972. Perinatal behavior of northern elephant seal females and their young. Behaviour 43:121-156.

MCCORMICK, H., AND T. ALLEN.
1963. Shadows in the sea. Chilton Books, Phila., 415 p.

MCCOSKER, J. E.
1981. Great white shark. Science 81 2(6):42-51.

MILLER, D. J., AND R. S. COLLIER.
1980. Shark attacks in California and Oregon, 1926-1979. Calif. Fish Game 67(2):76-104.

NISHIWAKI, M.
1972. General biology. *In* S. H. Ridgway (editor), Mammals of the sea: Biology and medicine, p. 3-204. Charles C. Thomas, Springfield, Ill.

TOWNSEND, C. H.
1885. An account of recent captures of the California sea-elephant, and statistics relating to the present abundance of the species. Proc. U.S. Natl. Mus. 8:90-93.

BURNEY J. LE BOEUF

Center for Coastal Marine Studies and Crown College
University of California, Santa Cruz
Santa Cruz, CA 95064

MARIANNE RIEDMAN

Center for Coastal Marine Studies
University of California, Santa Cruz
Santa Cruz, CA 95064

RAYMOND S. KEYES

Sea World
1720 South Shores Road
San Diego, CA 92109

VERTICAL STRATIFICATION OF THREE NEARSHORE SOUTHERN CALIFORNIA LARVAL FISHES (*ENGRAULIS MORDAX, GENYONEMUS LINEATUS,* AND *SERIPHUS POLITUS*)

Length measurements of larval fish are most frequently used in describing life stages (Moser and Ahlstrom 1974), and the subsequent development of population estimates (Kumar and Adams 1977). Field and laboratory observations are used to construct growth models of larval fishes, which are useful in predicting rates of growth under various environmental conditions (Hunter 1976). When combined with observations of larval abundance and distribution, length measurements can be indicators of both larval and adult ecology. Larval length-frequency data provide information about adult distribution and abundance, spawning periodicity, food preferences, and behavioral transitions that occur during development (Gjøsaetor and Saetre 1974; Tanaka 1974).

Larval length-frequency distributions of three species of fish were determined in conjunction with a study of the effects of a power plant offshore cooling water intake on local nekton populations. The three species chosen [northern anchovy, *Engraulis mordax* (Engraulididae); white croaker, *Genyonemus lineatus* (Sciaenidae); queenfish, *Seriphus politus* (Sciaenidae)] are among the most abundant adult fishes in the area, and are important links in the local trophic structure. The northern anchovy is important as forage for larger fishes and is fished commercially for manufacture of fish meal and oil. While the two sciaenid species have less commercial value, both are important as forage for larger species.

Materials and Methods

Samples were collected as part of a program of preoperational environmental studies at San Onofre Nuclear Generating Station (Fig. 1). In the area near the generating station (designated "treatment"), two transects extended over depths of 8 to 11 m and 12 to 15 m. Transects were also located in a "reference" area 5.8 km northwest. The two areas are similar in bottom topography and in the presence of a kelp bed just south of the outer transects. Each transect was 760 m in length. The two treatment transects and the two reference transects were each separated by 150 m. Monthly collections were made every 30±2 d from March 1978 through July 1979. Results for March through July samples for 1978 and 1979 are presented as mean values for the 2 yr combined.

Three vertical water column levels were sampled. The neuston was sampled, using a Manta net (Brown 1979). This net has a rectangular mouth (86 cm × 15 cm) and is designed to sample the upper 14 cm of the water column. The net filtered a volume of approximately 100 m^3 during each tow.

Midwater samples were taken with paired opening-closing 60 cm diameter circular bongo

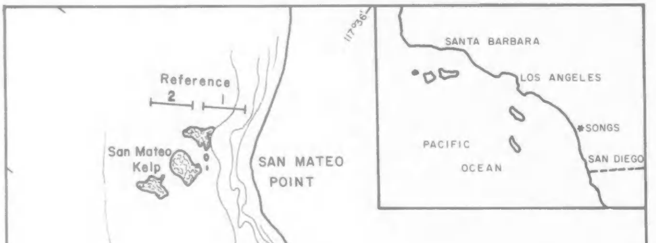

Reference
2
1
San Mateo Kelp
SAN MATEO POINT
117°36'
SANTA BARBARA
LOS ANGELES
SONGS
PACIFIC OCEAN
SAN DIEGO
N
117°33'
SAN ONOFRE NUCLEAR GENERATING STATION
33°23'
Treatment
2
1
San Onofre Kelp
33°22'
60
30
12
18
6
METERS
0 500 1000 2000
DEPTH IN FEET

FIGURE 1.—Location of sampling stations offshore San Onofre Nuclear Generating Station ("treatment") and San Mateo Point ("reference"). Inset locates the area in relation to southern California.

nets (McGowan and Brown 1966) towed obliquely through the entire midwater column (about 0.5 m below the surface to 1.0 m above the bottom). Each side of the paired net filtered a volume of about 200 m^3/tow.

Samples from the epibenthos were collected using an Auriga[1] net specially designed for sampling over rock-cobble bottoms. The net has a rectangular mouth, 0.5 m × 2.0 m, and filtered about 800 m^3 during each tow.

Each net was equipped with two flowmeters for volume determinations. Mesh size of each net was 0.333 mm, to facilitate collection of both eggs and larvae (Bolin 1936). Four replicates were collected by each gear at night at each of the four transects.

Due to shrinkage of the larvae during preservation (4% buffered Formalin-seawater), lengths of the individuals at hatching were smaller than those observed for unpreserved specimens (Theilacker 1980), ranging from 1.9 mm for white croaker to 2.5 mm for northern anchovy. The fish were considered to become juveniles after the development of adult fin rays and spines, which was taken as a length of 30 mm for all three species. Larvae were divided into 10 size classes of 3 mm each.

Results

Engraulis mordax

The major spawning period for northern anchovy was observed to be from December through May (Fig. 2). Length-frequency distributions in neuston samples indicated a pattern of high concentrations of small larvae during heaviest spawning periods (March and December 1978), followed by months of relatively even distributions from 0 to 15 mm. Larger larvae appeared and often became the major larval component in the neuston 2 to 3 mo after heavy spawning periods. Midsize larvae (12 to 18 mm) were often observed in reduced numbers in comparison with smaller or larger larval sizes. Low spawning activity during late summer was reflected in reduced numbers of larvae in neuston samples.

Midwater collections of northern anchovy were characterized by larval concentrations in the 6 to 18 mm size range, with abundance of 0 to 6 mm larvae fluctuating with spawning activity of adults. Except in the heavy spawning months of March and December 1978, midsize larvae generally outnumbered 2.5 to 6 mm larvae and composed the majority of midwater larvae taken. Significant numbers of larvae >21 mm were taken in the midwater samples only at the end of the main spawning season.

Collections of northern anchovy from epibenthic samples indicate consistent dominance of the distribution by 6 to 18 mm larvae during most months, with distributions shifted toward larger larvae during midsummer months. Overall concentrations in epibenthic samples were consistently the highest among the three levels.

Genyonemus lineatus

The major spawning period for white croaker was from December to May (Fig. 3). Larvae taken in the neuston were generally low in abundance and rarely larger than 6 mm, while midwater concentrations were also generally restricted to 0 to 6 mm larvae. Larvae were observed in these levels mainly from December through April. Most white croaker larvae were taken in epibenthic samples, especially late in the spawning season. In contrast to the upper two levels, larvae were relatively abundant from October through June. While small larvae were frequently taken in epibenthic samples during the major spawning months, the epibenthos was generally dominated by larvae in the 3 to 12 mm size range. Larvae >15 mm were rarely taken.

Seriphus politus

Queenfish, like white croaker, is highly seasonal in its spawning habits, with the main spawning period extending from March to September (Fig. 4). Significant numbers of larvae were taken in neuston collections only in March and April, and were restricted to 0 to 6 mm size classes. Midwater collections followed a similar trend, although slightly larger larvae persisted through September. The majority of queenfish larvae were taken in epibenthic samples, with numbers of individuals in each size class decreasing from 0 to 3 mm through 15 to 18 mm groups. As was observed in white croaker samples, individuals >18 mm were rarely collected.

---

[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

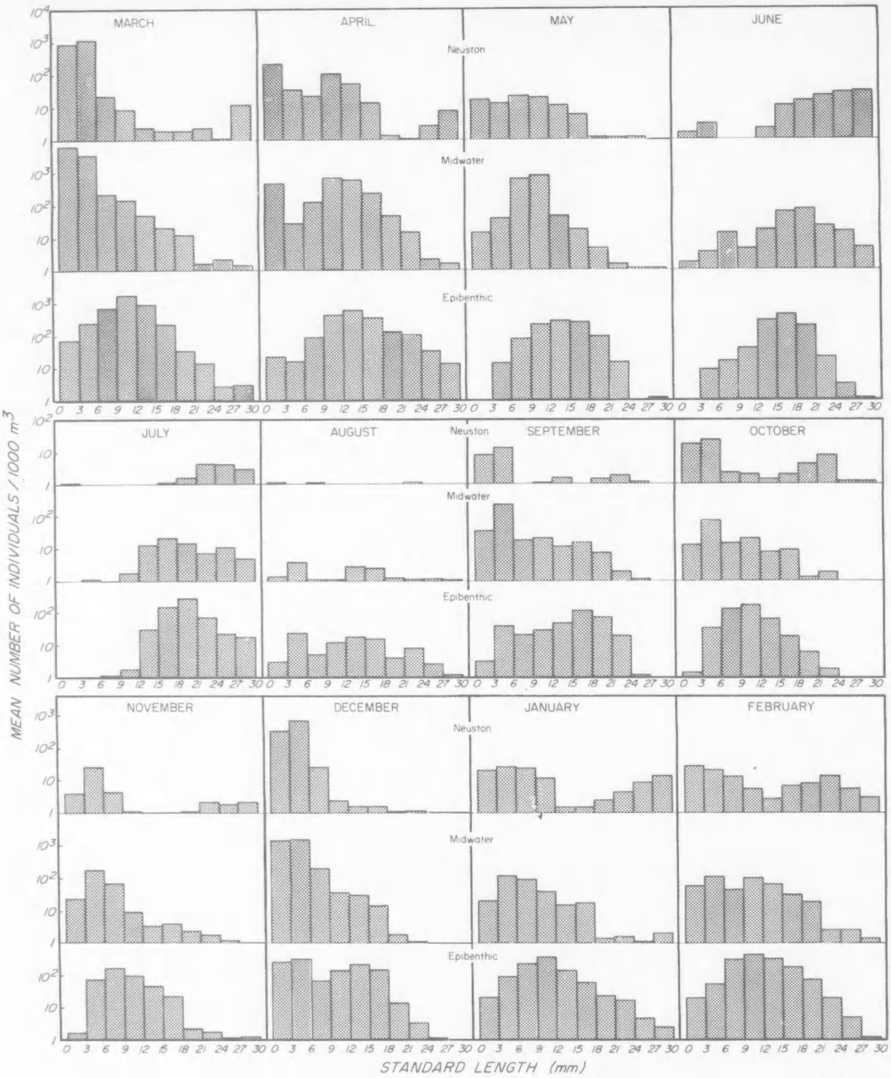


FIGURE 2.—Mean monthly concentrations of 10 larval size classes of northern anchovy, *Engraulis mordax*, in three water column levels, March 1978-February 1979. Each monthly value represents a mean of 4 replicates from each of 4 transects (total replicates = 16).

Discussion

In preliminary studies near San Onofre from August 1977 through February 1978, significantly greater numbers of larvae were observed in all three water column levels at night compared with daytime collections. Sampling was restricted to nighttime beginning in March 1978.

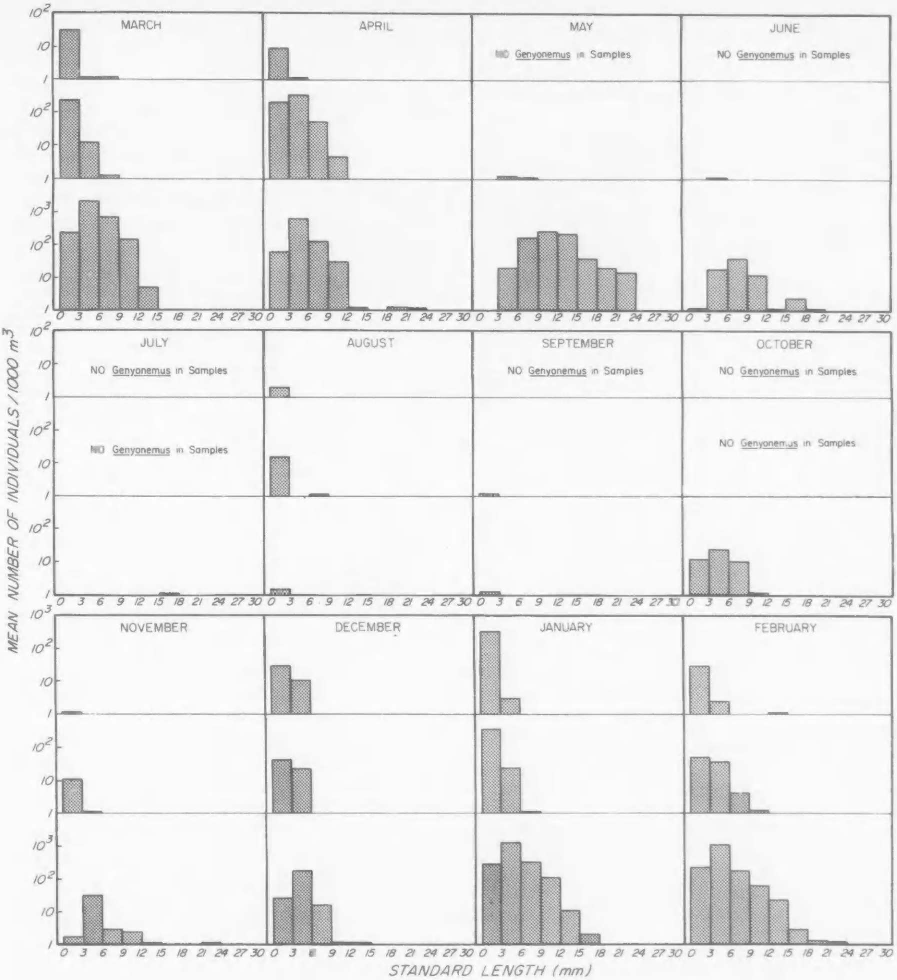


FIGURE 3.—Mean monthly concentrations of 10 larval size classes of white croaker, *Genyonemus lineatus*, in three water column levels, March 1978-February 1979. Each monthly value represents a mean of 4 replicates from each of 4 transects (total replicates = 16).

During the course of the study, no relationship between larval abundance and distribution and tidal stage, sea state, or stage of the moon was noted.

Vertical length-frequency distributions of all three species examined appear to be related to mode of feeding of each larval species, development during life history, and availability of food in the study area. The relationship between food availability and survival of larval northern anchovy is well documented. Larval anchovy require cells of 40 μm diameter in concentrations near 30 particles/ml (Lasker 1975, 1978). Lasker (1975) observed extensive feeding of anchovy larvae at the chlorophyll maximum layer, and Hunter and Thomas (1974) stated that anchovy

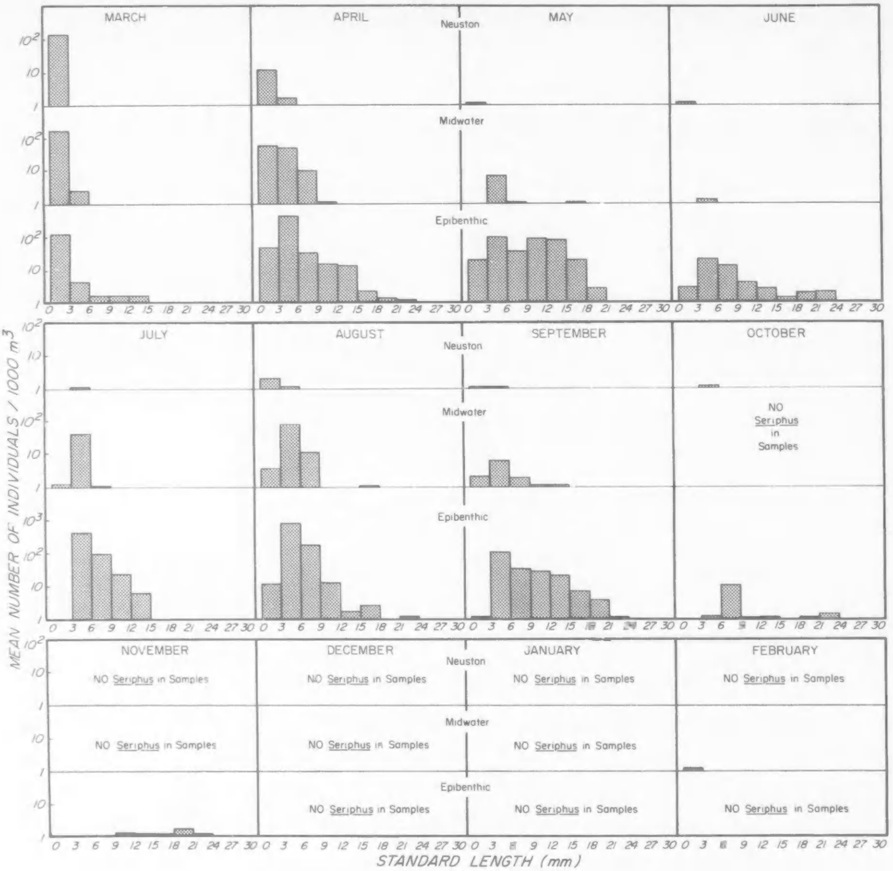


FIGURE 4.—Mean monthly concentrations of 10 larval size classes of queenfish, *Seriphus politus*, in three water column levels, March 1978-February 1979. Each monthly value represents a mean of 4 replicates from each of 4 transects (total replicates = 16).

larvae seek and remain in patches of the dinoflagellate *Gymnodinium splendens* in both day and night. Vertical differences in anchovy larval concentrations were shown by Ahlstrom (1959) to correspond to the level of the thermocline. In the San Onofre nearshore region, the maximum depths of the sampled transects were only 11 to 15 m, and the vertical zone is substantially compressed compared with offshore waters. Studies have indicated high concentrations of food in this nearshore area (Barnett and Sertic 1979). Concentrations of chlorophyll a 1 m below the surface and 1 m above the bottom were nearly equal during all times of the year from August 1976 to September 1978 at depths of 7 to 8 m and 18 to 30 m off San Onofre. Because adequate food may exist throughout the water column, a range of size classes is encountered at all depths. The apparent downward movement of larger anchovy larvae appears to be a natural behavioral response.

White croaker and queenfish larvae migrate toward the bottom after hatching. This vertical movement is associated with their adult life history, which is benthic in nature (Goldberg 1976). Additionally, larvae of 3 to 15 mm length of both these species feed primarily on zooplankton, which have been shown to be most abundant near the bottom in the nearshore San Onofre area (Barnett and Sertic 1979).

The absence of queenfish larvae in the neuston during the summer, and low concentrations in the midwater compared with the epibenthic level during the same period, may be due to the formation of the thermocline (density gradient) preventing eggs from entering the upper water column prior to hatching. Larvae of *G. lineatus* are more prevalent in these levels during the winter, when the water column is well mixed.

Length-frequency distributions of all three larval species are dependent on spawning cycles and behavioral and feeding patterns. Length-frequency distributions are reasonably accurate indicators of spawning periods, dependent on the life history of the species in question. Larvae of larger size classes are generally prevalent during periods of lowest abundance, after the main spawning period ends. During spawning periods, the distribution is dominated by smaller larvae. In distributions of northern anchovy, which apparently spawns intermittently year-round in the San Onofre region, the variability of the length-frequency median from month to month is highest in the neuston net and lowest in the epibenthos. Northern anchovy larvae apparently migrate from the neuston soon after hatching, but return upon reaching lengths of about 20 mm. Superimposed on spawning cycles, this phenomenon induces a high degree of variability to length-frequency medians of neuston samples. Larvae of the two sciaenid species, however, are benthic in nature, leading to increased variability in epibenthic samples, where the majority of these larvae are collected. At any one time, the major determining factor regulating the length-frequency distribution of these larval species near San Onofre is the reproductive state of each of the species.

Literature Cited

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

BARNETT, A. M., AND P. D. SERTIC.
1979. Spatial and temporal patterns of temperature, nutrients, seston, chlorophyll *a* and plankton off San Onofre, August 1976-September 1978, and the relationships of these patterns to the SONGS cooling system and preliminary report of patterns of abundance of ichthyoplankton off San Onofre and their relationship to the cooling operations of SONGS. Prepared for the Marine Review Committee of the California Coastal Commission. MRC Document 79-01, 250 p.

BOLIN, R. L.
1936. Embryonic and early larval stages of the California anchovy, *Engraulis mordax* Girard. Calif. Fish Game 22:314-321.

BROWN, D. M.
1979. The Manta net: quantitative neuston sampler. Univ. Calif. Scripps Inst. Oceanogr. Inst. Mar. Res. Tech. Rep. 64, 15 p.

GJØSAETER, J., AND R. SAETRE.
1974. The use of data on eggs and larvae for estimating spawning stock of fish populations with demersal eggs. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 139-150. Springer-Verlag, N.Y.

GOLDBERG, S. R.
1976. Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*. Fish. Bull., U.S. 74:983-984.

HUNTER, J. R.
1976. Culture and growth of the northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

HUNTER, J. R., AND G. L. THOMAS.
1974. Effect of prey distribution and density on the searching and feeding behaviour of larval anchovy *Engraulis mordax* Girard. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 559-574. Springer-Verlag, N.Y.

KUMAR, K. D., AND S. M. ADAMS.
1977. Estimation of age structure of fish populations from length-frequency data. *In* W. Van Winkle (editor), Assessing the effects of power-plant-induced mortality on fish populations, p. 256-281. Proceedings of the conference sponsored by Oak Ridge National Laboratory, Energy Research and Development Administration, and the Electric Power Research Institute, 3-6 May 1977. Pergamon Press, N.Y.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:212-230.

MCGOWAN, J. A., AND D. M. BROWN.
1966. A new opening-closing paired zooplankton net. SIO (Univ. Calif. Scripps Inst. Oceanogr.) Ref. 66-23, 56 p.

MOSER, H. G., AND E. H. AHLSTROM.
1974. The role of larval stages in systematic investigations of marine teleosts: The Myctophidae, a case study. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 605-608. Springer-Verlag, N.Y.

TANAKA, S.
1974. Significance of egg and larval surveys in the studies of population dynamics of fish. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 151-158. Springer-Verlag, N.Y.

THEILACKER, G. H.
1980. Changes in body measurements of larval northern

anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull., U.S. 78:685-692.

ROBERT E. SCHLOTTERBECK
DAVID W. CONNALLY

MBC Applied Environmental Sciences
947 Newhall Street
Costa Mesa, CA 92627

DECREASE IN LENGTH AT PREDOMINANT AGES DURING A SPAWNING MIGRATION OF THE ALEWIFE, *ALOSA PSEUDOHARENGUS*[1]

The spawning migration of the anadromous alewife, *Alosa pseudoharengus*, has been characterized by a decreasing trend in size and age. Cooper (1961) reported a trend in decreasing size in Pausacaco Pond, R.I., and Kissil (1974) found this one year in a 2-yr study at Bride Lake, Conn. A trend of decreasing size and age composition was also found in the Damariscotta River, Maine, alewife migration for the years 1977 through 1979 (Libby 1981).

Since 1977, data have been collected for length, weight, sex, age, and daily catch from the Damariscotta River commercial fishery. Analysis resulted in length-weight relationships, length, sex and age compositions, and an overall view of the annual stock changes. Further analysis of the collected data revealed that as age of the alewives decreased during migration, lengths at age also decreased with time. The analysis was applied only to 1979 and 1980 because of insufficient data in the other years.

The intent of this paper is to show the analysis and explain in greater detail this trend in decreasing length at age of an alewife migration.

The Study Area

The Damariscotta River alewife fishery is located approximately 29 km from the mouth of the river at the head of tide (Fig. 1). The river terminates at Great Salt Bay where a small outflow stream connects it with Damariscotta Lake.

Alewives are harvested with traps consisting of moveable metal bins that are set into the stream. Alewives swim into these bins which are then hoisted out of the water and the fish are dumped into a holding trough. The alewives that escape capture may pass through a fishway and

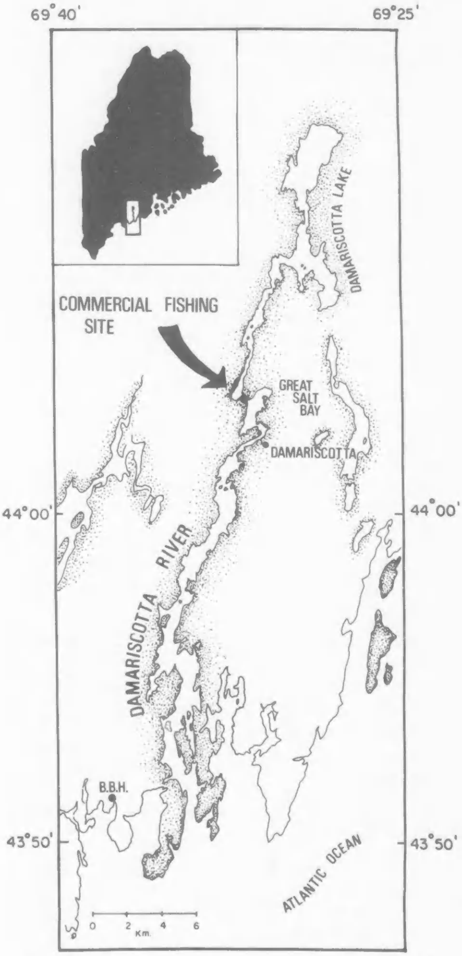


FIGURE 1.—Damariscotta River and site of the commercial alewife fishery.

---

[1] This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 89-304, as amended, Commercial Fisheries Research and Development Act, Projects AFC-21-1 and AFC-22-2.

into the lake to spawn. This particular fishery is one of about 30 commercially harvested alewife runs on the Maine coast and produces between 20 and 30% of the state's landings.

Materials and Methods

The method of harvesting was not considered selective of size, sex, or age of the alewives, and the catch presumably represented the true composition of the migrating stock. From previous work it was known that the size and age composition was not homogeneous throughout the run (Libby 1981), so a catch sample of fish was taken on alternate days to gain an equal representation of the total run.

Each sample consisted of 50 fish scooped from the catch in the holding trough. The sample was then brought to the laboratory and processed as soon as possible to minimize shrinkage or weight loss. Total length and weight were measured to the nearest millimeter and 0.1 g, respectively. The alewives were sexed by visual inspection of the gonads.

Otoliths were removed, cleaned, dried, and set into labeled black Plexiglas[2] trays. Watson (1965) described this procedure for mounting otoliths with the use of ethylene dichloride to fix the otoliths permanently in the trays. I prefer Permount, a histological medium that is poured over the otoliths and left to harden. If an otolith has to be repositioned, a drop of xylene will dissolve the Permount back to a liquid state. The otoliths were read with the use of a binocular microscope at a 30×-60× magnification.

Results and Discussion

The 1980 commercial harvest for the Damariscotta River lasted for 34 d, starting 4 May and ending 6 June. Fifteen daily samples were taken, each sample containing about 50 alewives totaling 365 males and 346 females. In each sample the sex ratio did not deviate significantly ($P>0.05$) based on a χ^2 test from a 1:1 ratio (Table 1). This ratio had been previously shown to be consistent from 1977 to 1979 in the Damariscotta River (Libby 1981).

TABLE 1.—Sex ratios and mean length of 15 alewife samples taken from the 1980 Damariscotta River commercial fishery.

Date	Sex ratio M:F	No. sampled	Mean length			
			Males	SE	Females	SE
5/6	1.3:1	50	305.0	1.7	316.2	2.2
5/8	1.0:1	50	300.4	1.8	316.6	1.6
5/12	1.1:1	50	305.2	1.7	310.2	2.0
5/14	1.2:1	50	304.1	1.6	315.4	2.3
5/16	0.9:1	37	304.4	1.6	312.9	2.2
5/18	0.6:1	50	301.6	1.8	308.5	1.6
5/20	1.2:1	50	299.9	1.5	311.0	1.4
5/22	1.4:1	50	302.0	1.4	309.0	1.8
5/24	0.8:1	50	292.7	1.8	302.0	1.7
5/26	0.9:1	50	299.3	1.5	308.3	1.8
5/28	1.3:1	50	296.3	1.7	305.9	2.5
5/30	0.9:1	50	295.7	1.7	304.2	1.8
6/1	1.1:1	45	298.0	1.9	307.7	2.2
6/3	1.2:1	44	293.4	2.2	307.2	2.3
6/5	1.5:1	35	299.0	2.7	305.3	2.4

In analyzing length with time, I was more concerned with similarities between the slopes of lines comparing males and females than in differences between mean lengths. Using the 1980 data as an example, females were shown to be larger than males at a given age (Table 1). A covariance analysis (Table 2) revealed no significant differences between slopes of the lines for the two sexes at the 5% level. Even though the mean length varied daily, the compared length distribution in each sample was less variable. Bartlett's test of homogeneity demonstrated no significant differences between the residual variances ($\chi^2 = 3.59$, df $= 1$, $P>0.05$). A t-test of significance of slope (t equals a ratio of the slope to its standard error) applied to the pooled regression coefficient showed that the slope (-0.36) was significantly different from zero ($t = 9.36$, df $= 707$, $P<0.05$). The influx of male and female alewives into the river follows a similar pattern regardless of their size differences. Ages throughout the 1979 and 1980 samples ranged from 3 to 8 yr for 234 males and 3 to 9 yr for 259 females and from 4 to 7 yr for 361 males and 3 to 7 yr for 344 females, respectively.

TABLE 2.—Analysis of covariance of length by time regression for male and female alewives and test for nonzero pooled slope. Damariscotta River, 1980.

Treatment	Regression coefficient	df	Residual SS	Mean square
Males	−0.32	363	27,388.279	
Females	−0.40	344	31,754.933	
	within	707	59,143.212	83.65
Pooled	−0.36	708	59,217.604	
Difference between slopes		1	74.392	74.39
Comparison of slopes		[1]F = 0.89, df = 707 [2]P = 0.65		
Test of pooled slope coefficient		[3]B = −0.36 SE = 0.04 t = B/SE = 9.36		

[1]F test, ratio of mean square of difference between slopes to mean square of difference within slopes.

[2]Calculated probability, not significant at the 5% level.

[3]Pooled slope coefficient.

---

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Age distribution from the 1979 and 1980 samples

Age:	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*Total*
1979								
Males	5	134	79	11	4	1	—	234
Females	1	115	116	22	3	1	1	259
1980								
Males	—	116	221	22	2	—	—	361
Females	2	93	211	32	6	—	—	344

Age by time regressions for the 1980 data were computed for each sex and an analysis of covariance (Table 3) revealed no significant differences between the slopes. The pooled regression like the pooled length by time regression, showed a significant slope (−0.02) at the 5% level. These two nonzero slopes (length by time and age by time) are evidence of changes in mean size and mean age throughout this alewife migration. The slope of the length trend (−0.36) is greater and significantly different from the age trend slope (−0.02) at the 5% level. The daily age composition of alewives moving to their spawning ground is a result of the fish schooling by size.

Lengths were separated into respective age categories for both years and regressions were computed of the age-length relation over time for each sex (Fig. 2). This was not done for ages three and seven through nine because of the small sample size. Ages four, five, and six were predominant, constituting over 95% of all the fish in the samples. All regressions produced negative slopes, although regressions A and B in 1979 and C and D in 1980 (Fig. 2) proved their slopes to be nonsignificant from a zero slope.

An analysis of covariance applied to all regressions in each year showed no significant differences between slopes (Tables 4, 5). Apparently the nonsignificant slopes still contributed to the homogeneity of the combined slopes producing significant 1979 and 1980 pooled regression slopes of −0.24 and −0.21, respectively. These results show, along with the previously observed decrease in length with time and age with time of this alewife migration, that the length of fish at age also decreases with time. The fish that arrive

TABLE 3.—Analysis of covariance of age by time regressions for male and female alewives and test for nonzero pooled slope. Damariscotta River, 1980.

Treatment	Regression coefficient	df	Residual SS	Mean square
Males	−0.016	359	115.755	
Females	−0.021	342	137.007	
	within	701	252.872	0.36
Pooled	−0.019	702	253.127	
Difference between slopes		1	0.365	0.37
Comparison of slopes		$^1F =$ 1.01, df = 701 $^2P = 0.32$		
Test of pooled slope coefficient		$^3B = -0.02$ SE = 0.003 $t = B/SE = 7.49$		

[1] *F* test, ratio of mean square of difference between slopes to mean square of difference within slopes.

[2] Calculated probability, not significant at the 5% level.

[3] Pooled slope coefficient.

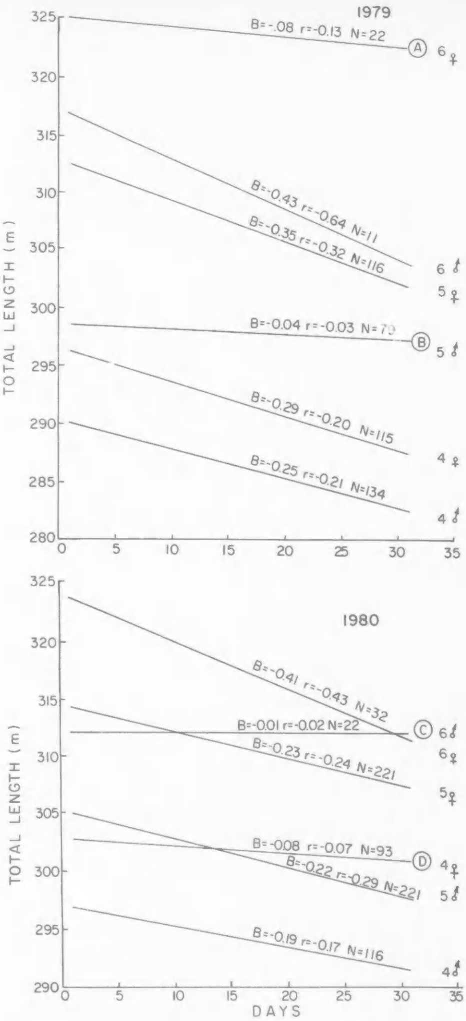


FIGURE 2.—Regressions of length at age with time from the 1979 and 1980 Damariscotta River alewife fishery.

TABLE 4.—Analysis of covariance of length by time regression by age and sex for alewives and test for nonzero pooled slope. Damariscotta River, 1979.

Treatment	Regression coefficient	df	Residual SS	Mean square
Male age				
4	−0.25	132	12,772.315	
5	−0.04	77	9,186.425	
6	−0.42	9	269.782	
Female age				
4	−0.29	113	11,810.600	
5	−0.35	114	11,923.360	
6	−0.08	20	996.642	
	within	465	46,959.124	100.10
Pooled	−0.24	470	47,503.000	
Difference between slopes		5	543.876	108.7
Comparison of slopes		$^1F = 1.07$, df $= 465$ $^2P = 0.63$		
Test of pooled slope coefficient		$^3B = -0.24$ SE $= 0.05$ $t = B/SE = 4.59$		

[1] *F* test, ratio of mean square of difference between slopes to mean square of difference within slopes.

[2] Calculated probability, not significant at the 5% level.

[3] Pooled slope coefficient.

TABLE 5.—Analysis of covariance of length by time regressions by age and sex and test for nonzero pooled slope. Damariscotta River, 1980.

Treatment	Regression coefficient	df	Residual SS	Mean square
Male age				
4	−0.19	114	7,819.279	
5	−0.22	219	10,575.189	
6	−0.01	20	835.044	
Female age				
4	−0.08	91	5,926.716	
5	−0.24	210	14,708.805	
6	−0.41	30	1,699.554	
	within	683	41,564.587	60.86
Pooled	−0.21	688	41,824.344	
Difference between slopes		5	259.757	51.95
Comparison of slopes		$^1F = 0.854$, df $= 683$ $^2P = 0.49$		
Test of pooled slope coefficient		$^3B = -0.21$ SE $= 0.03$ $t = B/SE = 6.15$		

[1] *F* test, ratio of mean square of difference between slopes to mean square of difference within slopes.

[2] Calculated probability, not significant at the 5% level.

[3] Pooled slope coefficient.

earliest are not only the largest of the migrating stock but also of the age groups.

The change in length at age is a source of bias in determining the age composition of the alewife harvest if a pooled age-length key were used. Westrheim and Ricker (1978) studied biases connected with application of an age-length key to stocks with different age compositions. Using an age-length key derived from pooled length subsamples will introduce bias in computing age composition of an anadromous alewife run. The pooled age-length key assumes homogeneity, but lengths at age change throughout the migration period. Such bias may, however, dwell within the range of acceptable error of 5% of the expected age frequencies. Chi square applied to each observed age frequency against the age-length key expected frequency, for each day sampled, indicated no significant differences between observed and expected age frequencies in the 1980 data. The magnitude of this decreasing trend in length at age may vary from year to year and stock to stock, but it is present and should be taken into account when investigating a migratory stock of alewives.

Acknowledgments

I thank David B. Sampson for his help and review of this paper, Sherry Collins for her assistance in data collecting, and James Rollins for drafting the figures.

Literature Cited

COOPER, R. A.
1961. Early life history and spawning migration of the alewife (*Alosa pseudoharengus*). M.S. Thesis, Univ. Rhode Island, Kingston, 58 p.

KISSIL, G. W.
1974. Spawning of the anadromous alewife, *Alosa pseudoharengus*, in Bride Lake, Connecticut. Trans. Am. Fish. Soc. 103:312-317.

LIBBY, D. A.
1981. Difference in sex ratios of the anadromous alewife, *Alosa pseudoharengus*, between the top and bottom of a fishway at Damariscotta Lake, Maine. Fish. Bull., U.S. 79:207-211.

WATSON, J. E.
1965. A technique for mounting and storing herring otoliths. Trans. Am. Fish. Soc. 94:267-286.

WESTRHEIM, S. J., AND W. E. RICKER.
1978. Bias in using an age-length key to estimate age-frequency distributions. J. Fish. Res. Board Can. 35: 184-189.

DAVID A. LIBBY

Department of Marine Resources
Marine Resources Laboratory
West Boothbay Harbor, ME 04575

SEASONAL SPAWNING CYCLE OF THE LONGFIN SANDDAB, *CITHARICHTHYS XANTHOSTIGMA* (BOTHIDAE)

This note contains the first description of the seasonal spawning cycle of the longfin sanddab, *Citharichthys xanthostigma*. This fish is common off southern California, but rare north of Santa Barbara and occurs at depths from 2 to 201 m (Miller and Lea 1976).

Methods

Fish were collected by otter trawl off the coast of southern California at depths of 45-64 m from San Clemente (lat. 33°20′N, long. 117°38′W) to Huntington Beach (lat. 33°40′N, long. 118°00′W). Collections were made during January-December 1978. Only females were examined. Specimens were immediately slit along the abdomen and placed in 10% Formalin[1]. Ovarian histological sections from 137 *C. xanthostigma* were cut at 8 μm and stained with iron hematoxylin. Seasonal gonosomatic indices (ovary wt/fish wt × 100) were calculated from preserved fish. Ovaries were classified histologically into four stages (Table 1).

TABLE 1.—Monthly distribution of body sizes (SL) and stages in *Citharichthys xanthostigma* spawning cycle, January-December 1978.

Month	*N*	Range (mm)	Regressed or regressing (%)	Previtellogenic (%)	Vitellogenic (%)	Spawning (%)
January	12	127-162	8	0	0	92
February	17	107-162	0	6	6	88
April	14	144-190	79	0	0	21
May	17	115-180	82	0	0	18
June	20	110-181	95	0	0	5
July	21	137-210	100	0	0	0
October	18	116-190	44	28	28	0
December	18	115-160	17	17	11	55

Results

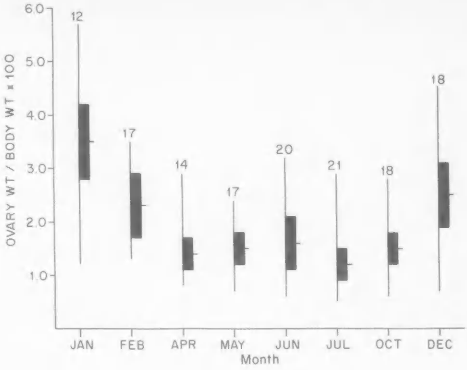


FIGURE 1.—Seasonal gonosomatic indices for *Citharichthys xanthostigma*. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval. Sample size above each month.

Most *C. xanthostigma* spawn in winter (Table 1). At this time the majority of females contain yolk-filled oocytes (>290 μm in diameter) and gonosomatic indices reach their highest values (Fig. 1). Females were in spawning condition in December. The presence of mature (yolk-filled) oocytes from an incipient spawning, and of postovulatory follicles which are remnants of the follicular walls of recently spawned oocytes (Hunter and Goldberg 1980), and of maturing oocytes for a subsequent spawning in the same ovary indicated that *C. xanthostigma* spawns more than once each season. The number of spawnings per season is unknown, however. Postovulatory follicles were similar to those of other teleost fishes (Hunter and Goldberg 1980). The smallest mature (ripe) female measured 107 mm SL (standard length); the largest, 181 mm SL. Miller and Lea (1976) reported this species may reach 250 mm TL (total length).

The incidence of spawning females decreased in spring. At this time most females contained regressed ovaries (Table 1) consisting of primary oocytes (53 μm) or regressing ovaries in which oocytes in various stages of vitellogenesis were undergoing atresia. Ovaries from fish taken during July were regressed, and gonosomatic indices were reduced (Fig. 1). Ovarian activity for the new spawning cycle began during autumn. This was apparent in October (Table 1) when previtellogenic females containing slightly enlarged, vacuolated oocytes (118 μm) and vitellogenic females (yolk deposition in enlarging oocytes) were present.

Discussion

My data have shown *C. xanthostigma* is a winter spawner in southern California. Spawning times in other California flatfishes are variable with a tendency toward winter. Fitch and Lavenberg (1971) reported the following spawning periods: *Platichthys stellatus*, November-February; *Microstomus pacificus*, November-March; *Citharichthys sordidus*, July-September; *Paralichthys californicus*, February-July. Goldberg (1981) reported summer spawning in *Symphurus atricauda* and summer-fall spawning (Goldberg 1982) in *Hippoglossina stomata*. Spawning in *Citharichthys stigmaeus* occurs April-September (Ford 1965). *Pleuronichthys verticalis* which was investigated by Fitch (1963) and Goldberg (1982) and *Glyptocephalus zachirus* which Frey (1971) reported on were in spawning condition throughout the year. Such year-round spawning is uncommon among California flatfishes.

---

[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Acknowledgments

I am grateful to M. Heinz and T. Pesich (Orange County Sanitation District, Marine Laboratory) and R. Sewell (Orange County Board of Education, Marine Studies Institute) for assistance in obtaining specimens. This study was aided by a Whittier College faculty research grant.

Literature Cited

FITCH, J. E.
1963. A review of the fishes of the genus *Pleuronichthys*. Los Ang. Cty. Mus. Contrib. Sci. 76:1-33.

FITCH, J. E., AND R. J. LAVENBERG.
1971. Marine food and game fishes of California. Univ. Calif. Press, Berkeley, 179 p.

FORD, R. E.
1965. Distribution, population dynamics and behavior of a bothid flatfish, *Citharichthys stigmaeus*. Ph.D. Thesis, Univ. Calif., San Diego, 243 p.

FREY, H. W. (editor).
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, 148 p.

GOLDBERG, S. R.
1981. Seasonal spawning cycle of the California tonguefish, *Symphurus atricauda* (Cynoglossidae). Copeia 1981:472-473.
1982. Seasonal spawning cycles of two California flatfishes, *Pleuronichthys verticalis* (Pleuronectidae) and *Hippoglossina stomata* (Bothidae). Bull. Mar. Sci. 32: 347-350.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77: 641-652.

MILLER, D. J., AND R. N. LEA.
1976. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 249 p. (Rev. publ. by Div. Agric. Sci., Univ. Calif., Richmond).

STEPHEN R. GOLDBERG

Department of Biology
Whittier College
Whittier, CA 90608

OTTER TRAWL SAMPLING BIAS OF THE GILL PARASITE, *LIRONECA VULGARIS* (ISOPODA, CYMOTHOIDAE), FROM SANDDAB HOSTS, *CITHARICHTHYS* SPP.

Lironeca vulgaris (Crustacea, Isopoda, Cymothoidae) is a common parasite infesting the gill chambers of many marine fish species from the California coast. Both male and female isopods reside in the gill chambers of sanddab hosts. Aspects of the ecology of this parasite and host specificity are given in Brusca (1978, 1981) and Keusink (1979). Both authors discuss the propensity of isopods, particularly males, to abandon hosts in otter trawls, which may cause false host records. Further, if host abandonment occurs during the trawling operation then estimates of prevalence (no. of infested hosts/total no. of hosts), relative parasite density (total no. of parasites/total no. of hosts), and mean parasite intensity (total no. of parasites/no. of infested hosts) will be biased. During a study of the interactions between *L. vulgaris* and two sanddab hosts, *Citharichthys stigmaeus* and *C. sordidus*, I analyzed the efficiency of traditional otter trawl collecting methods. Prevalence, relative parasite density, and mean parasite intensity were compared for samples of a host population gathered by otter trawls and divers utilizing scuba.

Methods

Speckled sanddabs, *Citharichthys stigmaeus*, and Pacific sanddabs, *C. sordidus*, were collected from a site about 0.5 km west of Goleta Point, Santa Barbara County, Calif., just seaward of an extensive bed of giant kelp, *Macrocystis pyrifera*. The depth was 16 m and the substrate consisted of fine sands and silts with occasional stands of the brown alga, *Pterygophora californica*, and patches of eelgrass, *Zostera marina*.

On 6 November 1979, five consecutive otter trawls of 10-min duration each were taken. The 3.7 m otter trawl was equipped with a cod end of 1.8 cm square mesh. Immediately following retrieval of the catch, sanddabs were sorted and placed in sealed plastic bags. Any *L. vulgaris* wandering about the catch were also retained. After the last trawl, four scuba divers entered the water and collected sanddabs by hand net, attracting fish with bait (sea urchin roe). Fish were transferred to sealed plastic bags. Specimens were collected in this manner for approximately 40 min. All fish and isopods collected by both methods were sexed and measured within the next day.

Host sex, total length to the nearest 0.1 cm, and number of parasitic isopods harbored were determined. Isopod total length was measured to the nearest 0.1 mm. Isopod sex was determined by several criteria: 1) Differential allometric relationship of width to length (Montalenti 1941), 2) presence of penes in males, 3) asymmetry of females, i.e., body twisted to the right or left (Brusca 1978), and 4) presence of oostegites in gravid females. Manca and aegathoid stages (see Brusca 1978) were lumped as juveniles.

Results and Discussion

Otter trawl catches consisted only of flatfish, and sanddabs comprised most of the catch. Size-frequency histograms for sanddab hosts collected by otter trawls and scuba divers were not significantly different (Fig. 1, Kolmogorov-Smirnov test, $P>0.05$). Inspection of these histograms indicates that divers are able to sample small fish more efficiently. Consequently, important information regarding the acquisition of isopod parasites by young fish may not be obtained when sampling with otter trawls. A comparison of the percent of fish infested with *L. vulgaris* reveals a highly significant disparity between the two sampling methods. In the trawl, 21 out of 56 hosts (37.5%) were infested versus 54 out of 73 hosts (73.9%) in the diver sample (chi-square = 17.449, $P<0.005$).

Size-frequency histograms for all isopods recovered by both collecting methods were significantly different (Fig. 2, Kolmogorov-Smirnov test, $P<0.05$). If only male isopods were considered, the difference was very significant ($P<0.01$) while for female isopods there was no difference ($P>0.05$). Apparently male *L. vulgaris* abandon hosts in otter trawls prior to retrieval of the catch. This was especially evident for small males (Fisher exact test, $P = 0.0057$; small males <10.6 mm vs. large males ≥10.6 mm). Large males may also leave their hosts since a majority of large male isopods were unassociated with hosts in the trawl sample (13 out of 17 males, see Figure 2). In one trawl sample a pod of male isopods was found in the cod end indicating that these individuals did not have sufficient opportunity to escape. Female isopods have feeble crawling abilities (Brusca 1978) and do not appear to abandon hosts in trawls.

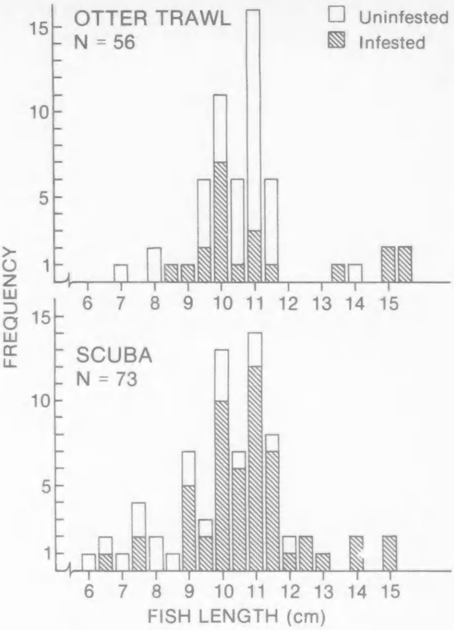


FIGURE 1.—Comparison of size-frequency histograms for *Citharichthys* spp. collected by otter trawl and divers utilizing scuba. Size distributions of sanddab hosts were similar (Kolmogorov-Smirnov test, $P>0.05$) but the percentage of hosts harboring parasitic isopods was significantly different (chi-square test, $P<0.005$).

Relative parasite density in the diver sample was significantly higher (1.2 isopods per fish) than otter trawl samples (0.4 isopods per fish) (t-test, $P<0.001$) as was mean parasite intensity with 1.6 and 1.1 isopods per infested host, respectively (t-test, $P<0.001$).

In conclusion, otter trawls consistently underestimate prevalence, relative parasite density, and mean parasite intensity of *L. vulgaris* popu-

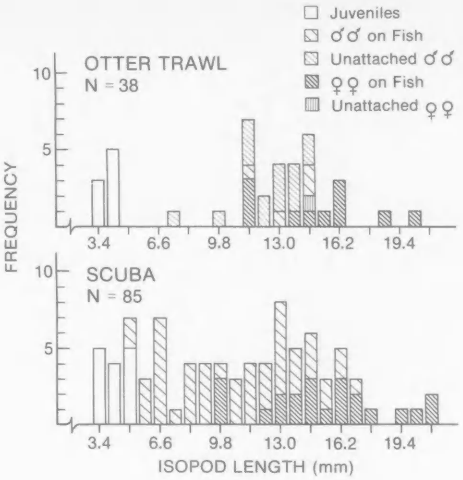


FIGURE 2.—Comparison of size-frequency histograms for the gill parasite, *Lironeca vulgaris*, from sanddab hosts collected by otter trawl and scuba divers. Size distributions of isopods were significantly different between the two samples (Kolmogorov-Smirnov test, $P<0.05$). Small male isopods were notably absent and several isopods were unattached to sanddab hosts in the otter trawl sample.

lations on *C. stigmaeus* and *C. sordidus*. This bias is caused by the abandonment of hosts, particularly by small male isopods. Shorter trawling times may reduce the amount of bias. However, when accuracy is desired, scuba is the preferred sampling method.

Acknowledgments

S. Anderson, D. Richardson, B. Harman, and S. Karl Kindly provided diving and trawling assistance. A. Kuris, R. Warner, G. Wellington, B. Victor, and M. Schildhaeur provided valuable comments on the manuscript.

Literature Cited

BRUSCA, R. C.
1978. Studies on the cymothoid fish symbionts of the eastern Pacific (Crustacea: Cymothoidae). II. Systematics and biology of *Lironeca vulgaris* Stimpson 1857. Occas. Pap. Allan Hancock Found., New Ser. 2:1-19.
1981. A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. Zool. J. Linn. Soc. Lond. 73:117-199.
KEUSINK, C.
1979. Biology and natural history of the fish parasite *Lironeca vulgaris* (Crustacea: Isopoda: Cymothoidae). M.A. Thesis, San Jose State Univ., San Jose, Calif.
MONTALENTI, G.
1941. Studi sull' ermafroditismo dei Cimotoidi. — I. *Emetha audouinii* (M. Edw.) e *Anilocra physodes* (L.). Publ. Stn. Zool. Napoli 18:337-394.

GARY R. ROBINSON

Department of Biological Sciences
University of California
Santa Barbara, Calif.
Present address: *Charles Darwin Research Station*
Santa Cruz Island, Galapagos
Casilla 58-39, Guayaquil, Ecuador

INDEX

Fishery Bulletin Vol. 80, 1-4

Acipenser oxyrhynchus—see Sturgeon, Atlantic

Acipenser transmontanus—see Sturgeon, white

Aerial surveys for manatees and dolphins in western peninsular Florida, by A. Blair Irvine, John E. Caffin, and Howard I. Kochman 621

Africa, northwest
  upwelling ecosystem
    regeneration of nitrogen by nekton 327

Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters, by Joanne Lyczkowski Laroche, Sally L. Richardson, and Andrew A. Rosenberg 93

Age and growth of larval Atlantic herring, *Clupea harengus* L., in the Gulf of Maine-Georges Bank region based on otolith growth increments, by R. Gregory Lough, Michael Pennington, George R. Bolz, and Andrew A. Rosenberg 187

AINLEY, DAVID G., HARRIET R. HUBER, and KEVIN M. BAILEY, Population fluctuations of California sea lions and the Pacific whiting fishery off central California 253

Alewife
  decrease in length at predominant ages during spawning migration 902

ALI, MOHAMMED LIAQUAT—see ULANOWICZ et al.

ALLEN, LARRY G., Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California 769

Alosa pseudoharengus—see Alewife

Analysis of double-tagging experiments, by Jerry A. Wetherall 687

Anarrhichthys ocellatus—see Eel, wolf

Anchovy, northern
  vertical stratification off southern California 895

ANGER, KLAUS, and RALPH R. DAWIRS, Elemental composition (C, N, H) and energy in growing and starving larvae of *Hyas araneus* (Decapoda, Majidae) 419

Antarctic Peninsula
  feeding ecology of some fishes 575

Arctica islandica—see Quahog, ocean

Argonata sp.
  association between, and aggregate salps 648

ARNOLD, CONNIE R.—see HOLT and ARNOLD

Ascelichthys rhodorus—see Sculpin, rosylip

(An) association between a pelagic octopod, *Argonauta* sp. Linnaeus 1758, and aggregate salps, by P. T. Banas, D. E. Smith, and D. C. Biggs 648

Atlantic Bight, Middle
  ocean quahog growth 21

Atlantic, northwest
  zooplankton
    effect of season and location on relationship between displacement volume and dry weight 631

Atlantic, western North
  whale, humpback
    feeding behavior 259

Atlantic Bight, South
  porgy, whitebone
    biology 863

Atlantic Ocean, western
  tuna, bluefin
    reproductive biology 121

(The) Atlantic sturgeon, *Acipenser oxyrhynchus*, in the Delaware River estuary, by Harold M. Brundage III and Robert E. Meadows 337

AU, D., and W. PERRYMAN, Movement and speed of dolphin schools responding to an approaching ship 371

Australia
  Gulf of Carpentaria
    effect of vertical migration on dispersal of penaeid shrimp larvae 541

Australia, Western
  lobster, rock
    stock and recruitment relationships 475

Avoidance of towed nets by the euphausiid *Nematoscelis megalops*, by P. H. Wiebe, S. H. Boyd, B. M. Davis, and J. L. Cox 75

BABINCHAK, JOHN A., DANIEL GOLDMINTZ, and GARY P. RICHARDS, A comparative study of autochthonous bacterial flora on the gills of the blue crab, *Callinectes sapidus*, and its environment 884

BAGLIN, RAYMOND E., JR., Reproductive biology of western Atlantic bluefin tuna 121

BAGLIVO, JENNY A.—see BROUSSEAU et al.

BAILEY, KEVIN M., The early life history of the Pacific hake, *Merluccius productus* 589

BAILEY, KEVIN M.—see AINLEY et al.

BANAS, P. T., D. E. SMITH, and D. C. BIGGS, An association between a pelagic octopod, *Argonauta* sp. Linnaeus 1758, and aggregate salps 648

BARANS, CHARLES A.—see MANOOCH and BARANS

BARSS, W. H.—see BOEHLERT et al.

Bass, striped
  bioenergetics and growth of embryos and larvae
    energy inputs 462, 463, 467
    energy outputs 463, 464, 470
    utilization efficiency 467
  effects of long-term mercury exposure on hematology 389

BATH, D. W., and J. M. O'CONNOR, The biology of the white perch, *Morone americana*, in the Hudson River estuary 599

BEACHAM, TERRY D., and PAUL STARR, Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia 813

(A) beak key for eight eastern tropical Pacific cephalopod species with relationships between their beak dimensions and size, by Gary A. Wolff 357

BIGGS, D. C.—see BANAS et al.

(The) biology of the white perch, *Morone americana*, in the Hudson River estuary, by D. W. Bath and J. M. O'Connor 599

Biology of the whitebone porgy, *Calamus leucosteus*, in the South Atlantic Bight, by C. Wayne Waltz, William A. Roumillat, and Charles A. Wenner 863

Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae, by Maxwell B. Eldridge, Jeannette A. Whipple, and Michael J. Bowers 461

Biscayne Bay, Florida
  interrelation of water quality, gill parasites, and gill pathology of some fishes 269

BLAXTER, J. H. S.—see COLBY et al.

BOEHLERT, GEORGE W., W. H. BARSS, and P. B. LAMBERSON, Fecundity of the widow rockfish, *Sebastes entomelas*, off the coast of Oregon 881

BOLZ, GEORGE R.—see LOUGH et al.

Bonnethead
  swimming kinematics 803

BOTSFORD, LOUIS W., RICHARD D. METHOT, JR., and JAMES E. WILEN, Cyclic covariation in the California king salmon, *Oncorhynchus tshawytscha*, silver salmon, *O. kisutch*, and Dungeness crab, *Cancer magister*, fisheries 791

BOWERS, MICHAEL J.—see ELDRIDGE et al.

BOYD, S. H.—see WIEBE et al.

British Columbia
  salmon, chum
    population biology, Fraser River 813

BRODEUR, RICHARD D.—see PETERSON et al.

BROUSSEAU, DIANE J., JENNY A. BAGLIVO, and GEORGE E. LANG, JR., Estimation of equilibrium settlement rates for benthic marine invertebrates: Its application to *Mya arenaria* (Mollusca: Pelecynoda) . 642

BRUNDAGE, HAROLD M., III, and ROBERT E. MEADOWS, The Atlantic sturgeon, *Acipenser oxyrhynchus*, in the Delaware River estuary 337

BURGESS, LOURDES ALVINA, Four new species of squid (Oegopsida: *Enoploteuthis*) from the central Pacific and a description of adult *Enoploteuthis reticulata* 703

CAFFIN, JOHN E.—see IRVINE et al.

Calamus leucosteus—see Porgy, whitebone

California, central
  sea lion, California
    population fluctuations and Pacific whiting fishery 253

California, southern
  croaker, white
    development of eggs and larvae off coast 403
  Newport Bay
    seasonal abundance, composition, and productivity of littoral fish assemblage 769
  salmon, coho
    phenotypic differences among hatchery and wild stocks 105
  shark, white
    predation on pinnipeds in coastal waters 891
  vertical stratification of nearshore larval fishes
    anchovy, northern 895
    croaker, white 895
    queenfish 895

Callinectes sapidus—see Crab, blue

Cancer magister—see Crab, Dungeness

Carcharhinus leucas—see Shark, bull

Carcharhinus melanopterus—see Shark, Pacific blacktip

Carcharodon carcharias—see Shark, white

CAREY, A. G., JR.,—see HOGUE and CAREY

CARTER, GARY R.—see HAIN et al.

CASEY, JOHN G.—see PRATT et al.

Cephalopods
  Pacific, eastern tropical
    beak key with relationships between beak dimensions and size 357

Cetaceans
  tagging techniques for small cetaceans
    freeze brands 137, 140
    natural marks 139, 140
    radio tags 136, 139
    Roto tags 140
    spaghetti tags 139, 140
    visual tags 136, 140

CHESTER, ALEXANDER J.—see HETTLER and CHESTER

CHITTENDEN, MARK E., JR.—see DeVRIES and CHITTENDEN; GEOGHEGAN and CHITTENDEN

Citharichthys cornutus
  larval development and occurrence
    cephalic spination 47
    characters, distinguishing 39
    counts 37
    developmental terminology 37
    fin and axial skeleton formation 44
    identification 38, 39
    morphometrics 37, 41
    occurrence 47
    pigmentation 40
    specimens 36
    teeth 47
    transformation 47

Citharichthys gymnorhinus
  larval development and occurrence
    cephalic spination 56
    characters, distinguishing 51
    counts 37
    developmental terminology 37
    fin and axial skeleton formation 54
    identification 38, 51
    morphometrics 37, 54
    occurrence 56
    pigmentation 51
    specimens 36
    teeth 56
    transformation 56

Citharichthys spilopterus
  larval development and occurrence
    cephalic spination 62
    characters, distinguishing 57
    counts 37
    developmental terminology 37
    fin and axial skeleton formation 61
    identification 38, 57
    morphometrics 37, 59
    occurrence 62
    pigmentation 57
    specimens 36
    teeth 62
    transformation 62

Citharichthys xanthostigma—see Sanddab, longfin

CLARKE, THOMAS A., Feeding habits of stomiatoid fishes from Hawaiian waters 287

CLIFFORD, DAVID A.—see CREASER and CLIFFORD

Clupea harengus—see Herring, Atlantic

Cod, Atlantic
  diet overlap between, and other northwest Atlantic finfish
    butterfish 749
    flounder, fourspot 751
    flounder, witch 751
    flounder, yellowtail 751
    haddock 751
    hake, red 749
    hake, spotted 749
    hake, silver 754
    hake, white 749
    plaice, American 751
    pollock 749
    pout, ocean 751
    redfish 747
    sculpin, longhorn 747
    scup 749
    skate, little 746

COLBY, DAVID R., DONALD E. HOSS, and J. H. S. BLAXTER. Pressure sensitivity of Atlantic herring, *Clupea harengus* L., larvae 567

COLIN, PATRICK L., Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae) 853

Columbia River
  Hanford, Washington
    snout dimorphism in white sturgeon 158

(A) comparative study of autochthonous bacterial flora on the gills of the blue crab, *Callinectes sapidus*, and its environment, by John A. Babinchak, Daniel Goldmintz, and Gary P. Richards 884

CONKLIN, ROBERT B.—see PRATT et al.

CONNALLY, DAVID W.—see SCHLOTTERBECK and CONNALLY

CONOVER, DAVID O., and STEVEN A. MURAWSKI, Offshore winter migration of the Atlantic silverside, *Menidia menidia* 145

COX, J. L.—see WIEBE et al.

Crab, blue
  comparative study of autochthonous bacterial flora on gills and environment 884

Crab, Dungeness
  cyclic covariation in California fisheries
    California, central, total catch 795
    California, northern
      catch by salmon species 794
      total catch 793
    switching effort between species 796

Crab, golden king
  larval description
    comparison of larval stages with descriptions by other authors 312
    stage I zoea 305
    stage II zoea 308
    stage III zoea 309
    stage IV zoea 309
    stage V (glaucothoe) 310

Crab, spider
  elemental composition and energy in growing and starving larvae
    biomass loss during starvation 427
    growth 420

Crab—see also *Cyclograpsus integer*

CRASS, DENNIS W., and ROBERT H. GRAY, Snout dimorphism in white sturgeon, *Acipenser transmontanus*, from the Columbia River at Hanford, Washington 158

CREASER, EDWIN P., and DAVID A. CLIFFORD, Life history studies of the sandworm, *Nereis virens* Sars, in the Sheepscot Estuary, Maine 735

Croaker, white
  eggs and larvae off southern California coast
    comparison with similar species 413
    distribution 415
    embryonic development 404
    fin development 410
    head spination 411
    ossification 411
    pigmentation 407
    proportions 413
    yolk-sac larvae morphology 407
    yolk-sac larvae pigmentation 405
  vertical stratification off southern California 895

Cyclic covariation in the California king salmon, *Oncorhynchus tshawytscha*, silver salmon, *O. kisutch*, and Dungeness crab, *Cancer magister*, fisheries, by Louis W. Botsford, Richard D. Methot, Jr., and James E. Wilen 791

Cyclograpsus integer H. Milne Edwards, 1837 (Brachyura, Grapsidae): The complete larval development in the laboratory, with notes on larvae of the genus *Cyclograpsus*, by Robert H. Gore and Liberta E. Scotto 501

Cyclograpsus integer
  larval development in laboratory
    fifth zoea (penultimate) 511
    fifth zoea (ultimate) 511
    first zoea 504
    fourth zoea 508
    megalopa 513
    rearing experiment results 502
    second zoea 505
    sixth zoea 513
    third zoea 508

Cynoscion nothus—see Seatrout, silver

DANIELS, ROBERT A., Feeding ecology of some fishes of the Antarctic Peninsula 575

DAVIS, B. M.—see WIEBE et al.

DAWIRS, RALPH R.—see ANGER and DAWIRS

DAWSON, MARGARET A., Effects of long-term mercury exposure on hematology of striped bass, *Morone saxatilis* 389

DEAN, J. M.—see RADTKE and DEAN

Decrease in length at predominant ages during a spawning migration of the alewife, *Alosa pseudoharengus*, by David A. Libby 902

Delaware River
  Atlantic sturgeon in estuary 337

Description of larvae of the golden king crab, *Lithodes aequispina*, reared in the laboratory, by Evan Haynes 305

Development and application of an objective method for classifying long-finned squid, *Loligo pealei*, into sexual maturity stages, by William K. Macy III 449

Development of eggs and larvae of the white croaker, *Genyonemus lineatus* Ayres (Pisces: Sciaenidae), off the southern California coast, by William Watson 403

Development of the vertebral column, fins and fin supports, branchiostegal rays, and squamation in the swordfish, *Xiphias gladius*, by Thomas Potthoff and Sharon Kelley 161

DeVRIES, DOUGLAS A., and MARK E. CHITTENDEN, JR., Spawning, age determination, longevity, and mortality of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico 487

Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish, by Richard W. Langton 745

Distribution, abundance, and age and growth of the tomtate, *Haemulon aurolineatum*, along the southeastern United States coast, by Charles S. Manooch III and Charles A. Barans 1

DIZON, ANDREW E.—see KAYA et al.

Dolphin, bottlenose
  Florida, western peninsular
    aerial surveys 621

Dolphin mortality
  estimating and monitoring incidental in eastern tropical Pacific
    combined kill-per-day and kill-per-ton method ... 398
    estimation procedures ... 397
    kill-per-day method ... 397
    kill-per-set method ... 399

Dolphin schools
  movement and speed, responding to an approaching ship
    school speed ... 376
    swimming behavior and school structure ... 377
    vessel avoidance ... 373

(The) early life history of the Pacific hake, *Merluccius productus*, by Kevin M. Bailey ... 589

Eel, wolf
  migration from Port Hardy, British Columbia, to Willapa Bay, Washington ... 650

(The) effect of protease inhibitors on proteolysis in parasitized Pacific whiting, *Merluccius productus*, muscle, by Ruth Miller and John Spinelli ... 281

Effect of season and location on the relationship between zooplankton displacement volume and dry weight in the northwest Atlantic, by Joseph Kane ... 631

Effects of long-term mercury exposure on hematology of striped bass, *Morone saxatilis*, by Margaret A. Dawson ... 389

ELDRIDGE, MAXWELL B., JEANNETTE A. WHIPPLE, and MICHAEL J. BOWERS, Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae ... 461

Elemental composition (C, N, H) and energy in growing and starving larvae of *Hyas araneus* (Decapoda, Majidae), by Klaus Anger and Ralph R. Dawirs ... 419

Engraulis mordax—see Anchovy, northern

Enoploteuthis spp.—see Squid

Estimating and monitoring incidental dolphin mortality in the eastern tropical Pacific tuna purse seine fishery, by Nancy C. H. Lo, Joseph E. Powers, and Bruce E. Wahlen ... 396

Estimation of equilibrium settlement rates for benthic marine invertebrates: Its application to *Mya arenaria* (Mollusca: Pelecynoda), by Diane J. Brousseau, Jenny A. Baglivo, and George E. Lang, Jr. ... 642

Etropus crossotus
  larval development and occurrence
    cephalic spination ... 67
    characters, distinguishing ... 63
    counts ... 37
    development terminology ... 37
    fin and axial skeleton formation ... 67
    identification ... 38, 62
    morphometrics ... 37, 64
    occurrence ... 67
    pigmentation ... 63
    specimens ... 36
    teeth ... 67
    transformation ... 67

Eubalaena glacialis—see Whale, right

(An) evaluation of techniques for tagging small odontocete cetaceans, by A. B. Irvine, R. S. Wells, and M. D. Scott ... 135

Fecundity of the widow rockfish, *Sebastes entomelas*, off the coast of Oregon, by George W. Boehlert, W. H. Barss, and P. B. Lamberson ... 881

Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic, by James H. W. Hain, Gary R. Carter, Scott D. Kraus, Charles A. Mayo, and Howard E. Winn ... 259

Feeding ecology of 0-age flatfishes at a nursery ground on the Oregon coast, by E. W. Hogue and A. G. Carey, Jr. ... 555

Feeding ecology of some fishes of the Antarctic Peninsula, by Robert A. Daniels ... 575

Feeding habits of stomiatoid fishes from Hawaiian waters, by Thomas A. Clarke ... 287

Finfish, northwest Atlantic
  diet overlap between
    Atlantic cod ... 745
    silver hake ... 745

Fish
  Maryland commercial landings
    identifying climatic factors influencing ... 611

Fish assemblage, littoral
  seasonal abundance, composition, and productivity in upper Newport Bay, California
    abiotic factors, influence ... 786
    catch, total ... 774
    cluster analysis and canonical correlation ... 773
    composition, diversity, and seasonal dynamics ... 784
    cumulative species curve ... 773, 774
    diversity ... 773
    production estimation ... 771
    productivity ... 779
    relationship of abiotic factors to fish abundance and distribution ... 783
    sampling procedures ... 771
    seasonal abundance and diversity ... 777
    species associations ... 777, 785
    species densities and productivity ... 785
    study area ... 770
    temperature and salinity patterns ... 773

Fish muscle
  trimethylamine estimation ... 157

- Fishery, deep-sea handline
  - multispecies analysis of commercial, in Hawaii
    - aggregation effects 444
    - clustering 439
    - data sources and fishery description 436
    - fishing effort 438, 440, 443
    - stock production analyses 441

- Fishes
  - Biscayne Bay, Florida
    - interrelation of water quality, gill parasites, and gill pathology 269
  - feeding ecology along Antarctic Peninsula
    - dietary similarity 583
    - diets 579
    - feeding behaviors 578
    - study area 575
  - nutrient requirements, qualitative and quantitative
    - amino acid availability 659
    - ascorbic acid 669
    - biotin 672
    - calcium 676
    - calcium-to-phosphorus ratios 676
    - carbohydrates 665
    - choline 671
    - copper 677
    - cyanocobalamin 671
    - fatty acids, essential 663
    - folic acid 671
    - inositol 672
    - iodine 678
    - iron 677
    - lysine 660
    - magnesium 676
    - manganese 677
    - methionine 660
    - niacin 668
    - optimal dietary lipid concentrations and protein-to-energy ratios 661
    - pantothenic acid 668
    - phosphorus 676
    - protein 656
    - pyridoxine 667
    - ribloflavin 667
    - selenium 678
    - thiamine 666
    - tryptophan 661
    - vitamin A 673
    - vitamin D 673
    - vitamin E 674
    - vitamin K 675
    - zinc 677
  - stomiatoid, feeding habits in Hawaiian waters
    - Astronesthidae 294
    - Chauliodontidae 294
    - Gonostomatidae 292
    - Idiacanthidae 296
    - Malacosteidae 298
    - Melanostomiatidae 296
    - Photichthyidae 291
    - Sternoptychidae 292

- Flatfishes
  - Oregon coast
    - feeding ecology of 0-age at nursery ground 555

Food habits of juvenile salmon in the Oregon coastal zone, June 1979, by William T. Peterson, Richard D. Brodeur, and William G. Pearcy 841

Four new species of squid (Oegospsida: *Enoploteuthis*) from the central Pacific and a description of adult *Enoploteuthis reticulata*, by Lourdes Alvina Burgess ... 703

Fundulus heteroclitus—see Mummichog

Gadus morhua—see Cod, Atlantic

Genyonemus lineatus—see Croaker, white

GEOGHEGAN, PAUL, and MARK E. CHITTENDEN, JR., Reproduction, movements, and population dynamics of the longspine porgy, *Stenotomus caprinus* 523

- Georgia, Strait of
  - herring fishery
    - case history of timely management aided by hydroacoustic surveys 381

GIBSON, D. M., A note on the estimation of trimethylamine in fish muscle 157

Ginglymostoma cirratum—see Shark, nurse

GOLDBERG, STEPHEN R., Seasonal spawning cycle of the longfin sanddab, *Citharichthys xanthostigma* (Bothidae) 906

GOLDMINTZ, DANIEL—see BABINCHAK et al.

GORE, ROBERT H., and LIBERTA E. SCOTTO, *Cyclograpsus integer* H. Milne Edwards, 1837 (Brachyura, Grapsidae): The complete larval development in the laboratory, with notes on larvae of the genus *Cyclograpsus* 501

GRAY, ROBERT H.—see CRASS et al.

Growth during metamorphosis of English sole, *Parophrys vetulus*, by Andrew A. Rosenberg and Joanne Lyczkowski Laroche 150

Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds, by Andrew A. Rosenberg 245

Growth of juvenile red snapper, *Lutjanus campechanus*, in the northwestern Gulf of Mexico, by Scott A. Holt and Connie R. Arnold 644

Growth of the ocean quahog, *Arctica islandica*, in the Middle Atlantic Bight, by Steven A. Murawski, John W. Ropes, and Fredric M. Serchuk 21

- Gulf of Carpentaria, Australia
  - shrimp larvae, penaeid
    - effect of vertical migration on dispersal 541

- Gulf of Mexico
  - seatrout, silver

    spawning, age determination, longevity, and mortality 487
  snapper, red
    growth of juvenile 644

Haemulon aurolineatum—see Tomtate

HAIN, JAMES H. W., GARY R. CARTER, SCOTT D. KRAUS, CHARLES A. MAYO, and HOWARD E. WINN. Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic 259

Hake, Pacific
  early life history
    development and growth 589
    development times 591
    growth rates 591
    metabolic rates 590, 593
    vertical distribution 590, 593

Hake, silver
  diet overlap, between other northwest Atlantic finfish
    butterfish 754
    cod, Atlantic 754
    flounder, fourspot 757
    flounder, witch 756
    flounder, yellowtail 757
    haddock 754
    hake, red 754
    hake, spotted 754
    hake, white 754
    plaice, American 756
    pollock 754
    pout, ocean 756
    redfish 752
    sculpin, longhorn 752
    scup 754
    skate, little 751

Hanford, Washington
  Columbia River
    snout dimorphism in white sturgeon 158

Hawaii
  fishery, deep-sea handline
    multispecies analysis, commercial 435
  fishes, stomiatoid
    feeding habits 287

HAYNES, EVAN. Description of larvae of the golden king crab, *Lithodes aequispina*, reared in the laboratory 305

HEINLE, DONALD R.—see ULANOWICZ et al.

Hemitripterus americanus
  trophic patterns among larvae in estuary 827

HENDRIX, SHARON D.—see KAYA et al.

Herring, Atlantic
  age and growth of larval based on otolith growth increments
    growth curve compared with other field studies . 196
    laboratory-reared larvae 191
    larval growth 194
    otolith growth 192
  pressure sensitivity 567

Herring fishery
  Strait of Georgia, timely management
    acoustic survey equipment and methods 382
    catch records 384
    1976-79 surveys 384-386
    spawning ground surveys 384
    trawling procedures, midwater 383

HETTLER, WILLIAM F., and ALEXANDER J. CHESTER. The relationship of winter temperature and spring landings of pink shrimp, *Penaeus duorarum*, in North Carolina 761

HJORT, R. C., and C. B. SCHRECK. Phenotypic differences among stocks of hatchery and wild coho salmon, *Oncorhynchus kisutch*, in Oregon, Washington, and California 105

Hogfish
  courtship and spawning observations 853
  egg and larval development 858
  egg collection and rearing 854
  spawning behavior 855
  spawning groups of *L. maximus* 855
  study site 854
  time and conditions of spawning 855

HOGUE, E. W., and A. G. CAREY, JR., Feeding ecology of 0-age flatfishes at a nursery ground on the Oregon coast 555

HOLT, SCOTT A., and CONNIE R. ARNOLD. Growth of juvenile red snapper, *Lutjanus campechanus*, in the northwestern Gulf of Mexico 644

HOSS, DONALD E.—see COLBY et al.

HUBER, HARRIET R.—see AINLEY et al.

Hudson River estuary
  perch, white
    biology 599

Hyas araneus—see Crab, spider

Identifying climatic factors influencing commercial fish and shellfish landings in Maryland, by Robert E. Ulanowicz, Mohammed Liaquat Ali, Alice Vivian, Donald R. Heinle, William A. Richkus, and J. Kevin Summers 611

Increment formation in the otoliths of embryos, larvae, and juveniles of the mummichog, *Fundulus heteroclitus*, by R. L. Radtke and J. M. Dean 201

(The) interrelation of water quality, gill parasites, and gill pathology of some fishes from south Biscayne Bay, Florida, by Renate H. Skinner 269

Invertebrates
  benthic marine
    equilibrium settlement rates 642

IRVINE, A. B., R. S. WELLS, and M. D. SCOTT. An evaluation of techniques for tagging small odontocete cetaceans 135

IRVINE, A. BLAIR, JOHN E. CAFFIN, and HOWARD I. KOCHMAN. Aerial surveys for manatees and dolphins in western peninsular Florida 621

JOLL, L. M.—see MORGAN et al.

JOYCE, GERALD G., JOHN V. ROSAPEPE, and JUNROKU OGASAWARA. White Dall's porpoise sighted in the North Pacific 401

KANE, JOSEPH. Effect of season and location on the relationship between zooplankton displacement volume and dry weight in the northwest Atlantic 631

Katsuwonus pelamis—see Tuna, skipjack

KAYA, CALVIN M., ANDREW E. DIZON, SHARON D. HENDRIX, THOMAS K. KAZAMA, and MARTINA K. K. QUEENTH. Rapid and spontaneous maturation, ovulation, and spawning of ova by newly captured skipjack tuna, *Katsuwonus pelamis* 393

KAZAMA, THOMAS K.—see KAYA et al.

KELLEY, SHARON—see POTTHOFF and KELLEY

KEYES, RAYMOND S.—see LE BOEUF et al; WEBB and KEYES

KNIGHT, MARGARET, and MAKOTO OMORI. The larval development of *Sergestes similis* Hansen (Crustacea, Decapoda, Sergestidae) reared in the laboratory 217

KOCHMAN, HOWARD I.—see IRVINE et al.

KRAUS, SCOTT D.—see HAIN et al.

Lachnolaimus maximus—see Hogfish

LAMBERSON, P. B.—see BOEHLERT et al.

LANG, GEORGE E., JR.—see BROUSSEAU et al.

LANGTON, RICHARD W., Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish 745

LAROCHE, JOANNE LYCZKOWSKI. Trophic patterns among larvae of five species of sculpins (Family: Cottidae) in a Maine estuary 827

LAROCHE, JOANNE LYCZKOWSKI, SALLY L. RICHARDSON, and ANDREW A. ROSENBERG. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters 93

LAROCHE, JOANNE LYCZKOWSKI—see ROSENBERG and LAROCHE

Larval development of *Citharichthys cornutus*, *C. gymnorhinus*, *C. spilopterus*, and *Etropus crossotus* (Bothidae), with notes on larval occurrence, by John W. Tucker, Jr. 35

Larval develoment of laboratory-reared rosylip sculpin, *Ascelichthys rhodorus* (Cottidae), by Ann C. Matarese and Jeffrey B. Marliave 345

(The) larval development of *Sergestes similis* Hansen (Crustacea, Decapoda, Sergestidae) reared in the laboratory, by Margaret Knight and Makoto Omori ... 217

LE BOEUF, BURNEY J., MARIANNE RIEDMAN, and RAYMOND S. KEYES. White shark predation on pinnipeds in California coastal waters 891

LEMBERG, NORMAN A.—see TRUMBLE et al.

LIBBY, DAVID A., Decrease in length at predominant ages during a spawning migration of the alewife, *Alosa pseudoharengus* 902

Life history studies of the sandworm, *Nereis virens* Sars, in the Sheepscot Estuary, Maine, by Edwin P. Creaser and David A. Clifford 735

Lironeca vulgaris
  otter trawl sampling bias of, from sanddab host ... 907

Lithodes aequispina—see Crab, golden king

LO, NANCY C. H., JOSEPH E. POWERS, and BRUCE E. WAHLEN. Estimating and monitoring incidental dolphin mortality in the eastern tropical Pacific tuna purse seine fishery 396

Lobster, rock
  stock and recruitment relationships in Western Australia
    breeding stock 478
    breeding stock abundance 476
    index of abundance of spawning stock 478
    juvenile abundance 477, 480
    juvenile densities and recruitment to the fishery . 482
    puerulus and juvenile densities 481
    puerulus settlement and subsequent spawning stock 482
    puerulus stage abundance 477, 480
    recruits to fishery abundance 477, 480
    spawning stock and puerulus settlement......... 480
    stock definition 477

Loligo pealei—see Squid, long-finned

Long Island, New York
  shark, white, observations off 153

LOUGH, R. GREGORY, MICHAEL PENNINGTON,

GEORGE R. BOLZ, and ANDREW A. ROSENBERG. Age and growth of larval Atlantic herring, *Clupea harengus* L., in the Gulf of Maine-Georges Bank region based on otolith growth increments 187

Lutjanus campechanus—see Snapper, red

MACY, WILLIAM K., III. Development and application of an objective method for classifying long-finned squid, *Loligo pealei*, into sexual maturity stages 449

Maine
  sculpins
    trophic patterns among larvae of five species in an estuary 827
  Sheepscot Estuary
    sandworm, life history studies 735

Manatee, West Indian
  Florida, western peninsular
    aerial surveys 621

MANN, ROGER. The seasonal cycle of gonadal development in *Arctica islandica* from the Southern New England shelf 315

MANOOCH, CHARLES S., III, and CHARLES A. BARANS. Distribution, abundance, and age and growth of the tomtate, *Haemulon aurolineatum*, along the southeastern United States coast 1

MARLIAVE—see MATARESE and MARLIAVE

Maryland
  fish and shellfish commercial landings
    climatic factors 611

Massachusetts
  whales, right
    Cape Cod waters 875

MATARESE, ANN C., and JEFFREY B. MARLIAVE. Larval development of laboratory-reared rosylip sculpin, *Ascelichthys rhodorus* (Cottidae) 345

MAYO, CHARLES A.—see HAIN et al.

MEADOWS, ROBERT E.—see BRUNDAGE and MEADOWS

Megaptera novaeangliae—see Whale, humpback

Menidia menidia—see Silverside, Atlantic

Mercury exposure
  bass, striped
    effects of long-term on hematology 389

Merluccius bilinearis—see Hake, silver

Merluccius productus—see Hake, Pacific; Whiting, Pacific

METHOT, RICHARD D., JR.—see BOTSFORD et al.

Migration of a juvenile wolf eel, *Anarrhichthys ocellatus*, from Port Hardy, British Columbia, to Willapa Bay, Washington. by David R. Miller 650

MILLER, DAVID R., Migration of a juvenile wolf eel, *Anarrhichthys ocellatus*, from Port Hardy, British Columbia, to Willapa Bay, Washington 650

MILLER, RUTH, and JOHN SPINELLI. The effect of protease inhibitors on proteolysis in parasitized Pacific whiting, *Merluccius productus*, muscle 281

MILLIKIN, MARK R., Qualitative and quantitative nutrient requirements of fishes: A review 655

MORGAN, G. R., B. F. PHILLIPS, and L. M. JOLL. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia 475

Morone americana—see Perch, white

Morone saxatilis—see Bass, striped

Movement and speed of dolphin schools responding to an approaching ship. by D. Au and W. Perryman .. 371

(A) multispecies analysis of the commercial deep-sea handline fishery in Hawaii. by Stephen Ralston and Jeffrey J. Polovina 435

Mummichog
  otolith increment formation
    age estimation of wild fish 210, 213
    effect of temperature and body growth on otolith formation 210, 213
    embryological formation 204, 206, 211
    light effect on increment formation 206, 212
    removal, preparation, and inspection 204

MURAWSKI, STEVEN A., JOHN W. ROPES, and FREDRIC M. SERCHUK. Growth of the ocean quahog, *Arctica islandica*, in the Middle Atlantic Bight . 21

MURAWSKI, STEVEN A.—see CONOVER and MURAWSKI

Mya arenaria
  equilibrium settlement rate estimation 642

Myoxocephalus aenaeus
  trophic patterns among larvae in estuary 827

Myoxocephalus octodecemspinosus
  trophic patterns among larvae in estuary 827

Myoxocephalus scorpius
  trophic patterns among larvae in estuary 827

Negaprion brevirostris—see Shark, lemon

Nekton
  regeneration of nitrogen in northwest Africa upwelling system
    excretion measurements 329

  nekton biomass 331
  regeneration rates 332

Nematoscelis megalops
 avoidance of towed nets 75

Nereis virens—see Sandworm

North Carolina
 shrimp, pink
  relationship of winter temperature and spring landings 761

(A) note on the estimation of trimethylamine in fish muscle, by D. M. Gibson 157

Observations of right whales, *Eubalaena glacialis*, in Cape Cod waters, by William A. Watkins and William E. Schevill 875

Observations on large white sharks, *Carcharodon carcharias*, off Long Island, New York, by Harold L. Pratt, Jr., John G. Casey, and Robert B. Conklin 153

Offshore winter migration of the Atlantic silverside, *Menidia menidia*, by David O. Conover and Steven A. Murawski 145

OGASAWARA, JUNROKU—see JOYCE et al.

OMORI, MAKOTO—see KNIGHT and OMORI

Oncorhynchus keta—see Salmon, chum

Oncorhynchus kisutch—see Salmon, coho; Salmon, silver

Oncorhynchus tshawytscha—see Salmon, chinook; Salmon, king

Oregon
 flatfishes
  feeding ecology of 0-age at nursery ground 555
 rockfish, widow
  fecundity off coast 881
 salmon, coho
  phenotypic differences among hatchery and wild stocks 105
 salmon, juvenile
  food habits in coastal zone, June 1979 841
 sole, English
  growth during metamorphosis 150

Otter trawl sampling bias of the gill parasite, *Lironeca vulgaris* (Isopoda, Cymothoidae), from sanddab hosts, *Citharichthys* spp., by Gary R. Robinson 907

Pacific, central
 squid
  four new species 703

Pacific, eastern tropical
 cephalopods
  beak key with relationships between beak dimensions and size 357
 dolphin mortality
  estimating and monitoring incidental in tuna purse seine fishery 396

Pacific, North
 white Dall's porpoise sighted 401

Panulirus cygnus—see Lobster, rock

Parophrys vetulus—see Sole, English

PEARCY, WILLIAM G.—see PETERSON et al.

Penaeus duorarum—see Shrimp, pink

PENNINGTON, MICHAEL—see LOUGH et al.

Perch, white
 biology in Hudson River estuary
  growth 602
  length conversions 602
  length-frequency and age distribution 602
  length-weight relationship 604
  reproduction 604
  sex ratio 606
  time of annulus formation 601

PERRYMAN, W.—see AU and PERRYMAN

PETERSON, WILLIAM T., RICHARD D. BRODEUR, and WILLIAM G. PEARCY, Food habits of juvenile salmon in the Oregon coastal zone, June 1979 841

Phenotypic differences among stocks of hatchery and wild coho salmon, *Oncorhynchus kisutch*, in Oregon, Washington, and California, by R. C. Hjort and C. B. Schreck 105

PHILLIPS, B. F.—see MORGAN et al.

Phocoenoides dalli—see Porpoise, Dall's

Pinnipeds
 California coastal waters
  predation by white shark 891

POLOVINA, JEFFREY J.—see RALSTON and POLOVINA

Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia, by Terry D. Beacham and Paul Starr 813

Population fluctuations of California sea lions and the Pacific whiting fishery off central California, by David G. Ainley, Harriet R. Huber, and Kevin M. Bailey 253

Porgy, longspine
 reproduction, movements, and population dynamics
  age determination and growth using length-frequency analysis 534
  age determination using scales 534
  maturation and spawning seasonality 525

- mortality and postspawning survival ... 536
- movements, spawning areas, and diel variation in catch ... 531
- size, maximum, and lifespan ... 536
- total weight-total length, girth-total length, and length-length relationships ... 537

Porgy, whitebone
- biology in South Atlantic Bight
  - age and growth ... 866
  - distribution and abundance ... 864
  - reproduction ... 868
  - South Carolina commercial landings ... 871

Porpoise, Dall's
- white, sighted in North Pacific ... 401

Port Hardy, British Columbia
- eel, wolf
  - migration of juvenile from, to Willapa Bay, Washington ... 650

POTTHOFF, THOMAS, and SHARON KELLEY. Development of the vertebral column, fins and fin supports, branchiostegal rays, and squamation in the swordfish, *Xiphias gladius* ... 161

POWERS, JOSEPH E.—see LO et al.

PRATT, HAROLD L., JR., JOHN G. CASEY, and ROBERT B. CONKLIN. Observations on large white sharks, *Carcharodon carcharias*, off Long Island, New York ... 153

Pressure sensitivity of Atlantic herring, *Clupea harengus* L., larvae, by David R. Colby, Donald E. Hoss, and J. H. S. Blaxter ... 567

Quahog, ocean
- growth in Middle Atlantic Bight
  - field studies ... 23
  - length-weight studies ... 28
  - mark-recapture studies ... 24
  - shell banding studies ... 26
- southern New England shelf
  - seasonal cycle of gonadal development ... 315

Qualitative and quantitative nutrient requirements of fishes: A review, by Mark R. Millikin ... 655

Queenfish
- vertical stratification off southern California ... 895

QUEENTH, MARTINA K. K.—see KAYA et al.

RADTKE, R. L., and J. M. DEAN, Increment formation in the otoliths of embryos, larvae, and juveniles of the mummichog, *Fundulus heteroclitus* ... 201

RALSTON, STEPHEN, and JEFFREY J. POLOVINA, A multispecies analysis of the commercial deep-sea handline fishery in Hawaii ... 435

Rapid and spontaneous maturation, ovulation, and spawning of ova by newly captured skipjack tuna, *Katsuwonus pelamis*, by Calvin M. Kaya, Andrew E. Dizon, Sharon D. Hendrix, Thomas K. Kazama, and Martina K. K. Queenth ... 393

Regeneration of nitrogen by the nekton and its significance in the northwest Africa upwelling ecosystem, by Terry E. Whitledge ... 327

(The) relationship of winter temperature and spring landings of pink shrimp, *Penaeus duorarum*, in North Carolina, by William F. Hettler and Alexander J. Chester ... 761

Reproduction, movements, and population dynamics of the longspine porgy, *Stenotomus caprinus*, by Paul Geoghegan and Mark E. Chittenden, Jr. ... 523

Reproductive biology of western Atlantic bluefin tuna, by Raymond E. Baglin, Jr. ... 121

RICHARDS, GARY P.—see BABINCHAK et al.

RICHARDSON, SALLY L.—see LAROCHE et al.

RICHKUS, WILLIAM A.—see ULANOWICZ et al.

RIEDMAN, MARIANNE—see LE BOEUF et al.

ROBINSON, GARY R., Otter trawl sampling bias of the gill parasite, *Lironeca vulgaris* (Isopoda, Cymothoidae), from sanddab hosts, *Citharichthys* spp. ... 907

Rockfish, widow
- fecundity off Oregon coast ... 881

ROPES, JOHN W.—see MURAWSKI et al.

ROSAPEPE, JOHN V.—see JOYCE et al.

ROSENBERG, ANDREW A., Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds ... 245

ROSENBERG, ANDREW A., and JOANNE LYCZKOWSKI LAROCHE. Growth during metamorphosis of English sole, *Parophrys vetulus* ... 150

ROSENBERG, ANDREW A.—see LAROCHE et al.; LOUGH et al.

ROTHLISBERG, PETER C., Vertical migration and its effect on dispersal of penaeid shrimp larvae in the Gulf of Carpentaria, Australia ... 541

ROUMILLAT, WILLIAM A.—see WALTZ et al.

Salmon, chinook
- food habits of juvenile in Oregon coastal zone, June 1979
  - diet overlap ... 847
  - occurrence and abundance of prey taxa ... 846

Salmon, chum
- food habits of juvenile in Oregon coastal zone, June

- 1979
  - diet overlap 847
  - occurrence and abundance of prey taxa 843
- population biology from Fraser River, British Columbia
  - age composition and sex ratios of returning adults 815
  - age of return 819
  - fecundity 816
  - fry migrations and survival 816
  - marine growth 815
  - return to escapement 820

Salmon, coho
- food habits of juvenile in Oregon coastal zone, June 1979
  - diet overlap 847
  - occurrence and abundance of prey taxa 843
- phenotypic differences among hatchery and wild stocks, U.S. Pacific coast
  - characters, morphological 107, 108
  - electrophoresis 107
  - environmental data 107
  - isozyme gene frequencies 110
  - life history 107, 110
  - sampling 106
  - statistics 108
  - stock similarity 113
  - stream systems and wild stocks similarity 117

Salmon, king
- cyclic covariation in California fisheries
  - California, central, total catch 795
  - California, northern
    - catch by salmon species 794
    - total catch 793
  - switching effort between species 796

Salmon, silver
- cyclic covariation in California fisheries
  - California, central, total catch 795
  - California, northern
    - catch by salmon species 794
    - total catch 793
  - switching effort between species 796

Sanddab
- otter trawl sampling bias of *Lironeca vulgaris* 907

Sanddab, longfin
- seasonal spawning cycle 906

Sandworm
- life history study in Sheepscot Estuary, Maine
  - eggs, numbers laid 738, 741
  - environmental conditions during spawning 738, 741
  - length frequency 737, 740
  - oocyte development 738, 741
  - predation 740
  - salinity and temperature of study area 737, 740
  - spawning characteristics 739, 742

SCHEVILL, WILLIAM E.—see WATKINS and SCHEVILL

SCHLOTTERBECK, ROBERT E., and DAVID W. CONNALLY, Vertical stratification of three nearshore southern California larval fishes (*Engraulis mordax, Genyonemus lineatus,* and *Seriphus politus*) 895

SCHRECK, C. B.—see HJORT et al.

SCOTT, M. D.—see IRVINE et al.

SCOTTO, LIBERTA E.—see GORE and SCOTTO

Sculpin, rosylip
- larval development
  - axial skelton 350
  - egg collection and laboratory rearing 345
  - fin development 350
  - identification 346
  - measurements 346
  - morphology 349
  - oral region 350
  - pigment patterns 347
  - reproductive behavior and larval rearing 353
  - spination 353

Sculpins
- trophic patterns among larvae in a Maine estuary
  - diet comparisons 830
  - diet composition 829
  - diet overlap 831
  - feeding incidence 829
  - mouth size, larval, and prey width 836

Sea lion, California
- California, central
  - population fluctuations and Pacific whiting fishery 253

Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California, by Larry G. Allen 769

(The) seasonal cycle of gonadal development in *Arctica islandica* from the Southern New England shelf, by Roger Mann 315

Seasonal spawning cycle of the longfin sanddab, *Citharichthys xanthostigma* (Bothidae), by Stephen R. Goldberg 906

Seatrout, silver
- spawning, age determination, longevity, and mortality in Gulf of Mexico
  - age determination using scales 494
  - distribution and availability 495, 498
  - growth and age determination 496
  - growth and age determination by length frequency 493
  - maximum size, life span, and mortality 495, 498
  - spawning 489, 496
  - total weight- and girth-standard length and standard length-total length relationships 495

Sebastes entomelas—see Rockfish, widow

SERCHUK, FREDRIC M.—see MURAWSKI et al.

- *Sergestes similis*
  - larval development
    - nauplius I 218
    - nauplius II 218
    - nauplius III 218
    - nauplius IV 223
    - postlarva I 238
    - postlarva II 238
    - protozoea I 223
    - protozoea II 223
    - protozoea III 225
    - zoea I 231
    - zoea II 234

- *Seriphus politus*—see Queenfish

- Shark, bull
  - swimming kinematics 803

- Shark, lemon
  - swimming kinematics 803

- Shark, leopard
  - swimming kinematics 804

- Shark, nurse
  - swimming kinematics 803

- Shark, Pacific blacktop
  - swimming kinematics 803

- Shark, white
  - observations off Long Island, New York 153
  - predation on pinnipeds in California coastal waters 891

- Sharks
  - swimming kinematics 803

- Shellfish
  - Maryland commercial landings
    - identifying climatic factors influencing 611

- Shrimp, pink
  - relationship of winter temperature and spring landings in North Carolina
    - air-water temperature relation 765
    - annual temperature cycle in Newport River Estuary 764
    - relationship between temperature, rainfall, and landings 765

- Shrimp larvae, penaeid
  - effect of vertical migration on dispersal in Gulf of Carpentaria, Australia
    - consequences of vertical migration 545
    - ontogeny of vertical migration 543
    - pattern variations of vertical distribution 544

- Silverside, Atlantic
  - migration, offshore winter 145

- SKINNER, RENATE H., The interrelation of water quality, gill parasites, and gill pathology of some fishes from south Biscayne Bay, Florida 269

- SMITH, D. E.—see BANAS et al.

- Snapper, red
  - Gulf of Mexico
    - growth of juvenile 644

- Snout dimorphism in white sturgeon, *Acipenser transmontanus*, from the Columbia River at Hanford, Washington, by Dennis W. Crass and Robert H. Gray 158

- Sole, English
  - age and growth in Oregon coastal waters
    - field and laboratory procedures 94
    - increment formation 95
    - spawning and rearing procedures 94
    - statistical procedures 95
  - growth during metamorphosis 150
  - growth in estuarine and open coastal nursery grounds 245

- Spawning, age determination, longevity, and mortality of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico, by Douglas A. DeVries and Mark E. Chittenden, Jr. 487

- Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae), by Patrick L. Colin 853

- *Sphyrna tiburo*—see Bonnethead

- SPINELLI, JOHN—see MILLER and SPINELLI

- Squid
  - *Enoploteuthis reticulata*
    - adult description 723
  - four new species from the central Pacific
    - bathymetric distribution 728
    - *Enoploteuthis higginsi* 718
    - *Enoploteuthis jonesi* 713
    - *Enoploteuthis obliqua* 704
    - *Enoploteuthis octolineata* 708
    - geographic distribution 728
    - key to species of *Enoploteuthis* 731
    - relationships 729

- Squid, long-finned
  - objective method for classifying into sexual maturity stages
    - application 453
    - biological relevance and accuracy 456
    - classification process 452
    - comparisons with other classification methods 457
    - discriminant functions development 451
    - maturity stages, four 453
    - multivariate approach, objectivity and utility 456

- STARR, PAUL—see BEACHAM and STARR

- *Stenotomus caprinus*—see Porgy, longspine

- Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia, by G. R. Morgan, B. F. Phillips, and L. M. Joll 475

(The) Strait of Georgia herring fishery: A case history of timely management aided by hydroacoustic surveys, by Robert J. Trumble, Richard E. Thorne, and Norman A. Lemberg 381

Sturgeon, Atlantic
- Delaware River estuary 337

Sturgeon, white
- Columbia River at Hanford, Washington
  - snout dimorphism 158

SUMMERS, J. KEVIN—see ULANOWICZ et al.

Swimming kinematics of sharks, by P. W. Webb and Raymond S. Keyes 803

Swordfish
- development
  - anal fin 169
  - anal fin pterygiophores 171
  - branchiostegal rays 179
  - caudal fin 172
  - caudal fin supports 172
  - dorsal fin 165
  - dorsal fin pterygiophores 166
  - pectoral fin 162
  - pectoral fin supports 163
  - squamation 181
  - vertebral column 175

Tagging experiments
- analysis of double-tagging
  - adjustment factor estimation for single-tag recoveries 692
  - models 689
  - mortality rate 699
  - parameter estimation of specific models 693
  - shedding rate and parameter estimation 691
  - tag loss in single-tagging experiments 687

Tagging techniques
- cetaceans, small odontocete 135

THORNE, RICHARD E.—see TRUMBLE et al.

Thunnus thynnus—see Tuna, bluefin

Tomtate
- distribution, abundance, and age and growth along southeastern U.S. coast
  - age and growth 3, 10, 15
  - distribution and relative abundance 1, 4, 14
  - length-weight and fork length-total length relationships 4, 13
  - management 16
  - mortality estimates 4, 13
  - spawning 4, 13, 16

Triakis semifasciata—see Shark, leopard

Trichechus manatus—see Manatee, West Indian

Triglops murrayi
- trophic patterns among larvae in an estuary 827

Trimethylamine
- estimation in fish muscle 157

Trophic patterns among larvae of five species of sculpins (Family: Cottidae) in a Maine estuary, by Joanne Lyczkowski Laroche 827

TRUMBLE, ROBERT J., RICHARD E. THORNE, and NORMAN A. LEMBERG, The Strait of Georgia herring fishery: A case history of timely management aided by hydroacoustic surveys 381

TUCKER, JOHN W., JR., Larval development of *Citharichthys cornutus, C. gymnorhinus, C. spilopterus,* and *Etropus crossotus* (Bothidae), with notes on larval occurrence 35

Tuna, bluefin
- reproductive biology of western Atlantic
  - egg diameter heterogeneity 126
  - fecundity estimates 131
  - gonosomatic index 123
  - morphology, gross 123
  - ova size 123
  - ovary histology 126
  - sex composition 123

Tuna, skipjack
- rapid and spontaneous maturation, ovulation, and spawning of ova by newly captured 393

Tursiops truncatus—see Dolphin, bottlenose

ULANOWICZ, ROBERT E., MOHAMMED LIAQUAT ALI, ALICE VIVIAN, DONALD R. HEINLE, WILLIAM A. RICHKUS, and J. KEVIN SUMMERS, Identifying climatic factors influencing commercial fish and shellfish landings in Maryland 611

Vertical migration and its effect on dispersal of penaeid shrimp larvae in the Gulf of Carpentaria, Australia, by Peter C. Rothlisberg 541

Vertical stratification of three nearshore southern California larval fishes (*Engraulis mordax, Genyonemus lineatus,* and *Seriphus politus*), by Robert E. Schlotterbeck and David W. Connally 895

VIVIAN, ALICE—see ULANOWICZ et al.

WAHLEN, BRUCE E.—see LO et al.

WALTZ, C. WAYNE, WILLIAM A. ROUMILLAT, and CHARLES A. WENNER, Biology of the whitebone porgy, *Calamus leucosteus,* in the South Atlantic Bight 863

Washington
- salmon, coho
  - phenotypic differences among hatchery and wild stocks 105

WATKINS, WILLIAM A., and WILLIAM E. SCHEVILL, Observations of right whales, *Eubalaena glacialis*, in Cape Cod waters 875

WATSON, WILLIAM, Development of eggs and larvae of the white croaker, *Genyonemus lineatus* Ayres (Pisces: Sciaenidae), off the southern California coast 403

WEBB, P. W., and RAYMOND S. KEYES, Swimming kinematics of sharks 803

WELLS, R. S.—see IRVINE et al.

WENNER, CHARLES A.—see WALTZ et al.

WETHERALL, JERRY A. Analysis of double-tagging experiments 687

Whale, humpback
  feeding behavior in western North Atlantic
    behavioral strategies 265
    bubbling behaviors 261
    circular swimming/thrashing 260
    inside loop behavior 261
    lunge feeding 260
    prey species 266

Whale, right
    observations in Cape Cod waters 875

WHIPPLE, JEANNETTE A.—see ELDRIDGE et al.

White Dall's porpoise sighted in the North Pacific, by Gerald G. Joyce, John V. Rosapepe, and Junroku Ogasawara 401

White shark predation on pinnipeds in California coastal waters, by Burney J. Le Boeuf, Marianne Riedman, and Raymond S. Keyes 891

Whiting, Pacific
  fishery off central California
    population fluctuations of California sea lions and 253

  protease inhibitors on proteolysis in parasitized muscle
    blended fish 282, 283
    diabasic phosphate peroxides 284
    effect of inhibition on texture 282, 285
    enzyme inhibitors 282
    fillet treatment 286
    frozen storage effect 285
    ground fish 282, 283
    hydrogen peroxide 284
    oxidative effect on amino acids 282, 285
    potassium bromate 284
    preparation of ground fish blocks for storage 282
    test for presence of peroxides or bromates 283

WHITLEDGE, TERRY E., Regeneration of nitrogen by the nekton and its significance in the northwest Africa upwelling ecosystem 327

WIEBE, P. H., S. H. BOYD, B. M. DAVIS, and J. L. COX, Avoidance of towed nets by the euphausiid *Nematoscelis megalops* 75

WILEN, JAMES E.—see BOTSFORD et al.

Willapa Bay, Washington
  eel, wolf
    migration of juvenile from Port Hardy, British Columbia, to 650

WINN, HOWARD E.—see HAIN et al.

WOLFF, GARY A., A beak key for eight eastern tropical Pacific cephalopod species with relationships between their beak dimensions and size 357

Xiphias gladius—see Swordfish

Zalophus californianus—see Sea lion, California

Zooplankton
  Atlantic, northwest
    effect of season and location on relationship between displacement volume and dry weight 631

NOTICES

NOAA Technical Reports NMFS published during first 6 months of 1982

Circular

442. Proceedings of the Sixth U.S.-Japan Meeting on Aquaculture, Santa Barbara, California, August 27-28, 1977. By Carl J. Sindermann (editor). March 1982, iii + 66 p. [Five articles are published in this paper.]
443. Synopsis of the biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. By Barbara Jayne Palko, Grant L. Beardsley, and William J. Richards. April 1982, iv + 28 p., 15 figs., 10 tables.
445. Sharks of the genus *Carcharhinus*. By J. A. F. Garrick. May 1982, vii + 194 p., 83 figs., 91 tables.

Special Scientific Report—Fisheries

753. Factors influencing ocean catches of salmon, *Oncorhynchus* spp., off Washington and Vancouver Island. By R. A. Low, Jr. and S. B. Mathews. January 1982, iv + 12 p., 6 figs., 7 tables.
754. Demersal fish resources of the eastern Bering Sea: Spring 1976. By Gary B. Smith and Richard G. Bakkala. March 1982, vi + 129 p., 92 figs., 68 tables.
755. Annotated bibliography and subject index on the summer flounder, *Paralichthys dentatus*. By Paul G. Scarlett. March 1982, iii + 12 p.
756. Annotated bibliography of the hard clam (*Mercenaria mercenaria*). By J. L. McHugh, Marjorie W. Sumner, Paul J. Flagg, Douglas W. Lipton, and William J. Behrens. March 1982, iii + 845 p.
757. A profile of the fish and decapod crustacean community in a South Carolina estuarine system prior to flow alteration. By Elizabeth Lewis Wenner, Malcolm H. Shealy, Jr., and Paul A. Sandifer. March 1982, iii + 17 p., 8 figs., 5 tables.

Some NOAA publications are available by purchase from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Individual copies of NOAA Technical Reports (in limited numbers) are available free to Federal and State Government agencies and may be obtained by writing to User Services Branch (D822), Environmental Science Information Center, NOAA, Rockville, MD 20852.

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including ZIP code.

The **abstract** should not exceed one double-spaced page.

In the **text**, *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual.* Fish names follow the style of the American Fisheries Society Special Publication No. 12, *A List of Common and Scientific Names of Fishes from the United States and Canada*, Fourth Edition, 1980.

Text footnotes should be typed separately from the text.

Figures and **tables**, with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¾ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (four double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited**. The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Serial Sources for the BIOSIS Data Base.* (*Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols**, such as mm, m, g, ml, mg, °C (for Celsius), %, ‰, and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
TEXT FOOTNOTES
APPENDIX
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Carl J. Sindermann, Scientific Editor
Fishery Bulletin
Northeast Fisheries Center
Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

Contents—continued

Notes

BOEHLERT, GEORGE W., W. H. BARSS, and P. B. LAMBERSON. Fecundity of the widow rockfish, *Sebastes entomelas*, off the coast of Oregon 881

BABINCHAK, JOHN A., DANIEL GOLDMINTZ, and GARY P. RICHARDS. A comparative study of autochthonous bacterial flora on the gills of the blue crab, *Callinectes sapidus*, and its environment 884

LE BOEUF, BURNEY J., MARIANNE RIEDMAN, and RAYMOND S. KEYS. White shark predation on pinnipeds in California coastal waters 891

SCHLOTTERBECK, ROBERT E., and DAVID W. CONNALLY. Vertical stratification of three nearshore southern California larval fishes (*Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*)................................ 895

LIBBY, DAVID A. Decrease in length at predominant ages during a spawning migration of the alewife, *Alosa pseudoharengus*............................ 902

GOLDBERG, STEPHEN R. Seasonal spawning cycle of the longfin sanddab, *Citharichthys xanthostigma* (Bothidae) 906

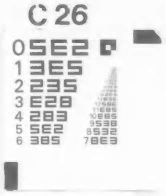
ROBINSON, GARY R. Otter trawl sampling bias of the gill parasite, *Lironeca vulgaris* (Isopoda, Cymothoidae), from sanddab hosts, *Citharichthys* spp. 907

INDEX, VOLUME 80 911

Notices

NOAA Technical Reports NMFS published during the first 6 months of 1982

* GPO 593-008



C 26
0 5E2
1 3E5
2 235
3 E28
4 283
5 5E2
6 385
7 8E3
8 532
9 538
10 E85
11 E85

TITLE: CUTIS

29 1-6
VOLUME: 30 ISSUES: 1-6

DATE: JANUARY - DECEMBER 1982

PUBLICATION NO: 7405

NOTES: INCLUDES INDEX

THIS PERIODICAL MAY BE COPYRIGHTED, IN WHICH CASE THE CONTENTS REMAIN THE PROPERTY OF THE COPYRIGHT OWNER. THE MICROFORM EDITION IS REPRODUCED BY AGREEMENT WITH THE PUBLISHER. DUPLICATION OR RESALE WITHOUT PERMISSION IS PROHIBITED.

UNIVERSITY MICROFILMS INTERNATIONAL, ANN ARBOR, MICHIGAN